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NEW ZEALAND SIDE-GILLED SEA SLUGS (OPISTHOBRANCHIA: NOTASPIDEA: PLEUROBRANCHIDAE)

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ABSTRACT

Five New Zealand species of the family Pleurobranchidae are recognized. *Berthella ornata* (Cheeseman) is endemic. *Bathyberthella zelandiae* is described as a new genus and species, and is also endemic. *Berthella aurantiaca* (Risso) is restricted to the Mediterranean Sea, but in New Zealand this name has been applied incorrectly and indiscriminately to two species differentiated here—*Berthellina citrina* (Rüppell & Leuckart) has a small shell, denticulate radular teeth, and possesses a prostate gland; *Berthella mediatas* Burn has a larger shell, smooth teeth and no prostate gland. *Pleurobranchaea maculata* (Quoy & Gaimard) is the sole species of its genus in New Zealand; *Pleurobranchaea novaezealandiae* Cheeseman and *Pleurobranchaea novaezelandiae* var. *granulosa* Bergh are synonyms of *P. maculata*.

Key words: Gastropoda; Opisthobranchia; Notaspidea; Pleurobranchidae; New Zealand; taxonomy; revision.

INTRODUCTION

Considerable advances have been made during the past decade in studies of nomenclature and relationships for New Zealand opisthobranchs. This paper reviews the order Notaspidea and in particular the family Pleurobranchidae. It arises from my investigations into the identity and ecology of shallow-water pleurobranchs from New Zealand (Willan, 1975) plus studies conducted since that time on additional material. These examinations extended the coverage to include deep-water species and thus this work now encompasses the entire New Zealand notaspidean fauna.

The Notaspidea have not been monographed before in New Zealand. Cheeseman (1878, 1879) was the only worker to describe pleurobranchs from New Zealand as new species. Others recorded side-gilled slugs from this country under the names of established species (Bergh, 1900; Odhner, 1924). These subsequent names were incorrect but inevitably became incorporated into important checklists of the New Zealand molluscan fauna (Suter, 1913; Powell, 1937, 1946, 1957, 1961, 1976, 1979) and so became entrenched. These incorrect taxa appeared in ecological works (Morton & Miller, 1968; Batham, 1969; Ottaway, 1977b). By noting that European names were being used incorrectly for New Zealand species, Burn (1962: 134) highlighted the taxonomic chaos that was the legacy of these early works.

Reviews and reappraisals of the genera *Pleurobranchella* Thiele (Willan, 1977), *Pleurobranchopsis* Verrill and *Gymnotoplax* Pilsbry (Willan, 1978) (none of which occurs in New Zealand) have already been published. This latter study was a prerequisite to this present paper in that it stabilized the taxonomy of *Berthellina* Gardiner. A review article on feeding within the Notaspidea that deals with two New Zealand species is currently in preparation.

MATERIALS AND METHODS

Material Studied

There are six species of the order Notaspidea in New Zealand; five belong to the Pleurobranchidae and one, *Umbraculum sinicum* (Gmelin, 1791), belongs to the Umbraculidae. *U. sinicum* is uncommon in this country and is found in northern waters only. As it has been described adequately from Australia by Burn (1959) and Thompson (1970), it is not treated further in this paper apart from its inclusion in the key.

All but one of the pleurobranchs occur in shallow water on the continental shelf. The taxonomic arrangement and sequence of

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TABLE 1. Classification of New Zealand pleurobranchs.

Family Pleurobranchidae
  Subfamily Pleurobranchinae
    Berthellina citrina (Rüppell & Leuckart, 1828)
    Berthella ornata (Cheeseman, 1878)
    Berthella mediatas Burn, 1962
    Bathyberthella zelandiae n. gen. & n. sp.
  Subfamily Pleurobranchaeinae
    Pleurobranchaea maculata (Quoy & Gaimard, 1832)

presentation in this publication are given in Table 1. Because of the past cursory descriptions of New Zealand pleurobranchs and lack of comparative details derived from anatomical examinations of specimens from this country I have described each species fully. Such detailed descriptions are required for all pleurobranchs before there is critical reappraisal of taxa as biologically meaningful entities.

Locality data of material examined for each species are given in the Appendix.

Terminology

Terminology used for describing the Notaspidea throughout this paper is as follows (Figs. 1–4). The terms refer specifically to pleurobranchs.

The body has a dorsal mantle and ventral foot; posteriorly the foot sometimes has a pedal gland ventrally and/or a caudal spur on the dorsal face. Body length (living specimens) is the distance between the middle of the anterior border of the oral veil and the posterior extremity of either the mantle or the foot, depending on which extends farther to the rear in the actively crawling animal. The prebranchial aperture, nephroproct and reproductive apertures are situated in front of the gill on the right side; the mouth opens anteriorly beneath an expanded oral veil, which is derived from a forward-projecting flap of tissue that grows outwards from, and yet remains connected to, the oral tentacles during metamorphosis (Gohar & Abul-Ela, 1957). The rhinophores are scroll-like and located above the oral veil.

The terminology of the gill requires standardization (Fig. 4). The axis of the gill is the rachis, which is either smooth or tuberculate. From the rachis smaller side branches arise alternately; these pinnae (= primary lamellae or pinnules) consist of an axis and a series of minute, overlapping leaves down each side. These side leaves are here called pinnules (= secondary lamellae or plicae). A membrane attaches the ventral surface of the rachis, for the greater part of its length, to the side of the body. Morton (1972) felt there was not enough evidence to homologize the gill of the Notaspidea with that of other opisthobranchs. He established that opisthobranchs have a wide variety of gill structures (e.g. the plicatidium of the Cephalaspidea and Anaspidea, the plume-like gill of the Notaspidea, and the circum-anal gills of the Doridacea) that replace the ctenidium of prosobranch molluscs.

Labelling of parts of the radular tooth follows Bertsch (1977), since the teeth of pleurobranchs are homologous to those of chromodorid nudibranchs. I follow Burn (1962) for terminology relating to the jaws and my labelling of reproductive organs incorporates the terminology proposed by Ghiselin (1965) for an idealized, gonochoric opisthobranch system.

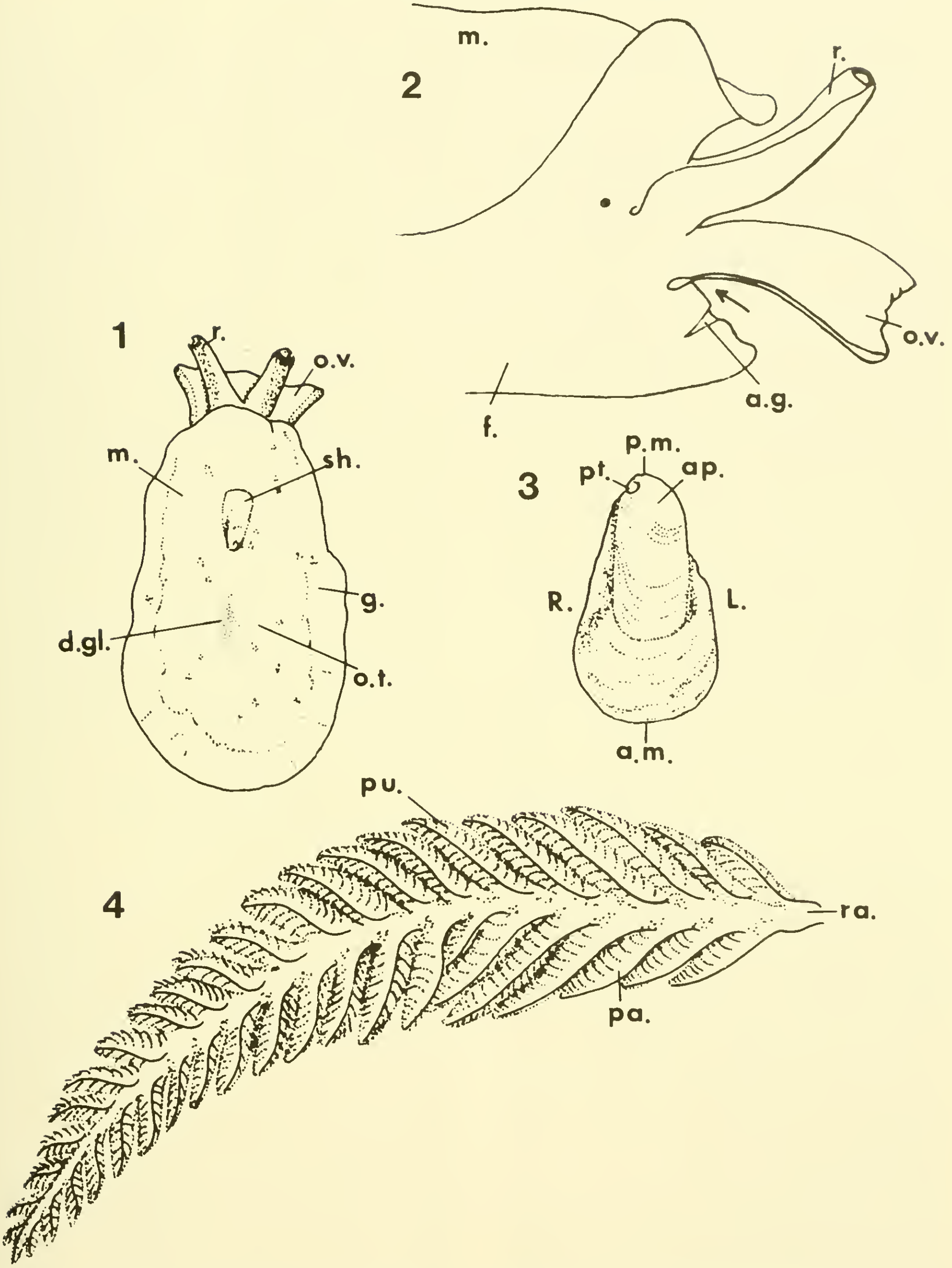
Many differences that have been used as generic characters are, in my view, only of use at the specific level. I list below those pleurobranch characters that have taxonomic value, and have attempted to assess their usefulness. Full information on all these characters, for both living and preserved animals where possible, is required in any future descriptions of pleurobranchs.

Mantle: Form, colour, extent and texture are distinctive and reasonably constant in living animals; these characters are most useful if there is some previous information on the degree of intraspecific variability.

Rhinophores: Very similar in construction throughout the group, all are scroll-like with a lateral groove and basal dilation. Data on size and position are of generic (rather than specific) value.

Oral veil: A most useful character to observe in living animals. Such features as relative width, strength of lateral extensions, degree of sinuosity and presence or absence of papillae on the anterior margin are good specific characters. All pleurobranchs have grooved edges to the lateral areas of the oral veil.

Foot and pedal structures: The foot offers the same types of characters as does the mantle. On the anterior dorsal surface a broad mucous gland and transverse slit are present. Some species possess a dorsal caudal spur and/or ventral gland towards the rear. The appearance of these structures probably indi-



FIGS. 1–4. Pleurobranch descriptive terminology. *Berthellina citrina* illustrated as a representative of the Pleurobranchidae. 1. Dorsal view of whole animal. 2. Lateral view of head; arrow indicates site of mouth. 3. Exterior of shell. 4. Lateral view of gill. Abbreviations. a.g. = mucous gland on anterior border of foot; a.m. = anterior margin of shell (i.e. edge facing anteriorly when shell is in place in living animal); ap. = apical region of teleoconch; d.gl. = digestive gland; f. = foot; g. = position of gill on right side beneath mantle; L. = left side of shell in place in living animal; m. = mantle; o.t. = ovotestis; o.v. = oral veil; pa. = pinna of gill; p.m. = posterior edge of shell (i.e. margin facing posteriorly when shell is in place in living animal); pt. = protoconch; pu. = pinnule of gill; R. = right side of shell in place in living animal; r. = rhinophore; ra. = rachis of gill; sh. = position of shell beneath mantle.

cates attainment of sexual maturity rather than similarity between species. The significance of these structures is discussed further at the end of this section.

Gill: The gill has been employed as an indicator of genus, depending whether the rachis is smooth or tuberculate (but I shall later query the importance of this feature). Generally the number of pinnae shows considerable intraspecific variation, particularly in relation to the size of the individual—juveniles have fewer pinnae and pinnules.

Shell: Presence or absence is important at the generic level; generally shape varies considerably within any one species. The shell is never wholly, or even partially, uncovered by the mantle in any pleurobranch when alive (Willan, 1978). In the literature are records of specimens of normally-shelled pleurobranchs being found without shells—*Pleurobranchus peroni* and *P. inhacae* (Macnae, 1962) and *Berthellina citrina* (Thompson, 1970; Edmunds & Thompson, 1972). So absence of a shell, by itself, should not be thought of as significant when an unknown specimen is being checked against a published description.

Gut: Pleurobranchs show little variation in the basic structure of the alimentary canal. Guiart (1901) used *Pleurobranchus membranaceus* (Montagu) in his description of the gut in the Pleurobranchidae, and Thompson & Slinn (1959) figured the alimentary canal of this species. Both the gut and nervous system are characteristic at the generic level.

Radula: Provides excellent diagnostic characteristics for delimiting genera (except *Pleurobranchus* and *Berthella*). Generally considerable intraspecific variation exists, particularly with respect to age of the individual (as is the case in doridacean nudibranchs—see Bertsch, 1976, 1977). Nevertheless, radular details are most useful at the species level when the extent of this variability is understood.

Jaws: As for the radula.

Reproductive system: A highly important source of differential characters at higher levels. From species to species there is variation in detail but it is easy to misinterpret developmental changes in the genital organs as specific differences.

Pedal gland: This enigmatic gland is found on many (maybe all) species of *Pleurobranchus, Berthella* and *Pleurobranchaea*. It was first described by Vayssière (1885), who attributed the first record of it to Delle-Chiaje (1828). Vayssière (1885: 111) was unable to suggest any function for the gland. Some steps have recently been made towards an understanding of the function of this gland. It is becoming clear that it has a sexual function. Thompson & Slinn (1959) showed that in *Pleurobranchus membranaceus* it is absent in juveniles but present in older specimens. Macnae (1962) noted the gland only in fully mature, sexually active specimens.

My observations on *Pleurobranchaea maculata* suggest that the appearance of this gland indicates the onset of sexual maturity. *P. maculata* reaches full size towards midwinter but there is no pedal gland. It appears when the water temperature rises in spring and remains until the animal dies the following summer. It thus seems that development of the gland takes place with attainment of sexual maturity. The shape of the gland varies considerably between species. I suggest that the gland produces a species-specific pheromone that diffuses through the water and draws members of the same species together to mate. Pleurobranchs tend to be solitary and widely scattered within one area, as dictated by their food; individuals are seldom found together except when copulating; it is possible, therefore, that there are chemical cues.

HIGHER CATEGORIES

Historical Overview

Pilsbry (1896) attempted the first synthesis of the Notaspidea. His system was based mostly on external characteristics. He recognized the Umbraculidae, with two genera and two subgenera, and the Pleurobranchidae, with six genera and two subgenera. Vayssière (1898,1901) published a large monograph dealing at length with the known pleurobranchs; his classification scheme had appeared earlier (Vayssière, 1896). The Pleurobranchidae were divided into four genera, one (*Pleurobranchus*) being further split into four subgenera. A second large monograph was written by Bergh (1897–1905), this work being produced quite independently from that of Vayssière. Bergh gave detailed anatomical accounts of specimens examined; however he did not treat all the known species as Vayssière had done. Bergh recognized six genera which he did not subdivide further. I have followed Winckworth (1946) in citing the dates of the five parts of Bergh's *Sempers*

Reisen, Malacologische Untersuchungen that deal with pleurobranchs.

Odhner (1926) presented another scheme, again based on external characteristics—pedal gland, gill rachis and mantle margin; within the Pleurobranchidae he recognized two subfamilies with a total of five genera and two subgenera. Marcus (1971) has translated Odhner's key into English. With some small alterations Odhner's classification has been kept by later reviewers (Thiele, 1931; Burn, 1962; Franc, 1968; Thompson, 1976); I use it here because it allows incorporation of the greatest number of features, including obvious external characteristics. Here I divide the Pleurobranchidae into two subfamilies with eight genera between them; recognition of subgenera is, in my opinion, premature at present. Mention must be made of Gardiner's (1936) brief paper, which because it reorganized generic nomenclature, was of great significance.

The order Notaspidea Fischer

All notaspideans have a single, elongate, plume-like gill on the right side of the body between the mantle and foot. All are carnivorous and have a broad radula with many teeth. All have rhinophores that are scroll-like and with a lateral, longitudinal slit. No species possesses parapodia. The order contains "tectibranchs" (with large, external, patelliform shells (Umbraculidae)), and "nudibranchs" (with shells that are internal or absent (Pleurobranchidae)). The Notaspidea form a transitional link between the lower (e.g. the shell-bearing Cephalaspidea) and higher (e.g. the shell-less Doridacea) opisthobranch groups. Evidence suggests that the Notaspidea represent an intermediate grade of organization. The shelled, umbraculiform members are so different anatomically from the pleurobranchs that both may well have reached the notaspidean state by independent paths from tectibranch ancestors.

Recently Thompson (1970, 1976) and Edmunds & Thompson (1972) have called this order Pleurobranchomorpha (originally a tribe of the order Opisthobranchia of Pelseneer (1906). I prefer to keep the name Notaspidea because it is brief and has been used consistently throughout the literature. Also, the other tribes which Pelseneer placed within the Opisthobranchia have been largely dismantled since. For example, Pelseneer included the Lophocercidae (now in Oxynoeidae, Sacoglossa) and Limacinidae, Cymbuliidae, Cavoliniidae (now in Thecosomata) in the tribe Bullomorpha. He included the Pneumodermatidae, Clionopsidae, Notobranchaeidae, Thiptodontidae, Clionidae, Halopsychidae (now in Gymnosomata) in the tribe Aplysiomorpha. It would appear more appropriate to use something other than Pleurobranchomorpha if a new name should be needed.

Thiele (1931) combined the Notaspidea with the Nudibranchia *sensu lato* in a new order, Acoela, to reflect their close relationships, the nudibranchs having risen from the pleurobranchs (Odhner 1939). But since the Notaspidea are so different from other groups of opisthobranchs they should be given equal ranking with the Nudibranchia. Furthermore, the homogeneity of the order Nudibranchia itself is in doubt (Minichev, 1970; Minichev & Starobogataov, 1978). Hyman (1967) noted that Thiele's taxonomy had failed to gain general acceptance, and most authors who have recently considered the arrangement of higher groups within the Opisthobranchia have given the Notaspidea ordinal status equal to that of the Nudibranchia *sensu lato* (Hyman, 1967; Minichev, 1970; Morton, 1958, 1972; Nordsieck, 1972; Taylor & Sohl, 1962; Thompson, 1976). Franc (1968), however, lists the order separately as Pleurobranchacea Deshayes, 1830.

Members of the order have long been recognized as falling into two distinct series, and I agree with Thompson (1976) that each warrants no less than subordinal ranking. The first (Umbraculacea) includes the family Umbraculidae Gray (= Umbrellidae auct.) with three genera: *Umbraculum* Schumacher, 1817; *Tylodina* Rafinesque, 1819; *Tylodinella* Mazzarelli, 1897.

The Umbraculidae is here diagnosed as follows:

Shell external, limpet-like, with protoconch minute and hyperstrophic, apex near centre, interior with a closed or incomplete muscle scar, periostracum often dense; body smaller or much larger than shell, mantle thin, margin serrated or tentaculate; foot with large flat sole, upper surface smooth or tuberculate; head with a pair of enrolled rhinophoral tentacles with sessile eyes at their bases, mouth with two pairs of small oral tentacles. Gill a long plume lying between mantle and foot on anterior and right side, adnate and bearing numerous bipinnate branches for greater part of its length, posterior end free and bipinnate;

anal papilla projecting behind attached portion of gill, penis anterior—external, lying in anterior sinus of foot, in median line in front of and below head (*Umbraculum*) or retractile, on right side in front of gill (*Tylodina, Tylodinella*). Radula very broad, bearing a great number of similar, crowded, needle-like teeth, with recurved simple cusps which lack subdenticles; buccal armature consisting of lightly cornified polygonal plates which lack subdenticles.

Some authors (Pruvot-Fol, 1954; Burn, 1959) divide the Umbraculidae into two families—Umbraculidae Dall and Tylodinidae Gray, on the basis of the proportions of the shell and body, and the position of the head (either projecting or included in an anterior sinus of the foot), and differences in external genitalia, shell periostracum and muscle scars, radula and buccal armature.

The Pleurobranchidae Menke

The second series (suborder Pleurobranchacea) constitutes the family Pleurobranchidae with seven recognized genera:

Pleurobranchus Cuvier, 1805 (*sensu* Thompson, 1970 and Baba & Hamatani, 1971)
Berthella Blainville, 1825
Pleurehdera Marcus & Marcus, 1970
Berthellina Gardiner, 1936
Pleurobranchaea Meckel in Leue, 1813
Euselenops Pilsbry, 1896
Pleurobranchella Thiele, 1925

The present work adds one more—*Bathyberthella* n. gen.

The Pleurobranchidae are defined as follows:

Gill on right side of body, extending backwards in groove between mantle and foot, rachis smooth or tuberculate, side pinnae subdivided into pinnules, anterior part attached to body by a basement membrane, posterior end free; prebranchial aperture in front of gill. Shell internal beneath mantle, either small or absent; when present the shell is haliotiform or spatulate. Mantle smooth or tuberculate, either large and separated from foot (*Pleurobranchus, Berthella, Pleurehdera, Berthellina, Bathyberthella*) or smaller than foot and merging with it anteriorly and/or posteriorly (*Pleurobranchaea, Euselenops, Pleurobranchella*). Head with trapezoidal oral veil projecting above mouth, its lateral edges longitudinally grooved; a pair of rolled rhinophores above oral veil, also laterally grooved, rhinophores arising either together mid-anteriorly or separately where mantle merges anteriorly into oral veil. Gut with extensible oral tube and muscular pharyngeal bulb inside which lie jaws and radula; two jaws placed laterally, composed of numerous similar imbricated mandibular elements; radula broad, with or without rachidian; gut with unpaired, dorsal oral gland opening anteriorly into pharyngeal bulb and a pair of salivary glands; tubules from oral gland ramify to a greater or lesser extent throughout the body; stomach a large, unthickened, mid-ventral sac; anus opening on right side. Animals hermaphroditic with diaulic or triaulic reproductive systems; penis retractile, stout or long and slender, sometimes with enclosing flaps externally and with or without penial gland internally, smooth or papillose; vas deferens with or without prostatic portion; eggs laid in loosely arranged, or coiled, spawn bands; larva hatching as a pelagic veliger. Distributed worldwide in tropical and temperate (rarely in cold) areas. The Pleurobranchidae have two subfamilies.

Pleurobranchinae Menke, 1828

Shell internal; distinct mantle with free edges all round; rhinophores arising together mid-anteriorly; radula without a rachidian; mandibular elements cruciform with simple or denticulate blades; generally low activity (but a few species are able to swim).

Pleurobranchaeinae Pilsbry, 1896

No shell; mantle reduced and continuous anteriorly with the oral veil, rhinophores separate, dorso-lateral; radula with or without rachidian; mandibular elements polygonal or scale-like and denticulate; generally high activity.

Burn (1962) elevated both to familial rank essentially on the presence or absence of a shell; but as Edmunds & Thompson (1972) have shown for *Berthellina citrina*, this character is not constant even within a species. My opinion is that these groups show such a unity of body design and gill plan and structure of the gut and reproductive system as to warrant placing them within a single family. These similarities suggest their derivation from a common ancestor.

Burn also split the Pleurobranchidae (*sensu* Burn, 1962) into two subfamilies—the Pleurobranchinae (large and with tuberculate gill rachis and pedal gland), and the Berthellinae (smaller with a non-tuberculate rachis and no pedal gland). These divisions are unjustified on the characters chosen since small species of Pleurobrachinae do exist, e.g. *Pleurobranchus ovalis* Pease (Thompson, 1970); some species of *Berthella* (subfamily Berthellinae) do have weak tubercles on the gill rachis, e.g. *B. ornata* (Cheeseman) (present observations); and several (if not all) species of *Berthella* have a pedal gland when they are sexually mature. Even though these groups do not warrant separation at the subfamilial level as advocated by Burn I agree with his distinctions and consider the "pleurobranchine" and "berthelline" groups represent natural lineages. The two monotypic genera *Pleurehdera* and *Bathyberthella* (the new genus described herein) together display all the characters required to span the gap between *Pleurobranchus* and *Berthellina*. I do not wish to imply, however, that either *Pleurehdera* or *Bathyberthella* is ancestral to either the "pleurobranchine" or the "berthelline" groups.

Relationships of genera within the Pleurobranchinae remain confused. I recognize only four (*Pleurobranchus, Berthella, Berthellina, Pleurehdera*) and add a fifth (*Bathyberthella*). I support Thompson (1970) and Baba & Hamatani (1971) in considering *Pleurobranchus* to encompass *Oscanius* Leach and *Susania* Gray. Two conflicting classifications for this subfamily have emerged from past studies; one based on radular characteristics unites *Berthella* and *Pleurobranchus* (e.g. Vayssière, 1896, 1898; Odhner, 1926), the other relying on the nature of the mantle, gill and shell unites *Berthella* and *Berthellina* and excludes *Pleurobranchus* (Burn, 1962). The two systems are incompatible. As stated above, my studies so far have led me to support the latter classification. Even though this stance is adopted, I acknowledge that *Pleurobranchus* and *Berthella* are close to each other. At present the only satisfactory character differentiating them is presence or absence, respectively, of tubercles on the mantle and gill rachis. When this character is set aside it seems impossible to draw a hard and fast line between them; indeed their radular and jaw structures seem identical. According to this criterion some species remain poised between *Pleurobranchus* and *Berthella* (the New Zealand *Berthella ornata* (Cheeseman) and North American *Berthella americana* (Dall) are examples). I suggest that difficulty of separating them has arisen more through lack of critical appraisal of species than lack of distinguishing characters. Species belonging to both genera require further examination (particularly for characters related to mantle, radula, jaws, reproductive and alimentary systems) that will enable the boundary to be cut more sharply if these genera are to remain separate.

Pleurobranchus and *Berthella* have long been upheld as separate. Both are enormous genera, easily the largest in the order, each has more than 50 named species although no one is sure how many biological species exist.

Pleurehdera (with its type species, *P. haraldi,* still known from only a single specimen from the Tuamotu Archipelago) and *Bathyberthella* are particularly important because they possess characters linking them with both pleurobranchine and pleurobranchaeine genera. One or both could be a key between the major genera or subfamilies. An appraisal of *Bathyberthella* with regard to other genera appears later in this work in connection with the description of the new species from New Zealand.

Despite the natural affinity of *Berthellina* and *Berthella* there are sufficient characters presently recognized to adequately diagnose them as separate. All species of *Berthellina* have immediately recognizable radulae, their shells too are distinctive; they have a prostate gland and jaws with (almost always) smooth mandibular elements. Were it not for its mandibular elements and pedal gland, *Pleurehdera haraldi* would be classified as a *Berthellina.* In all these characters *Berthellina* species differ from the *Pleurobranchus-Berthella* group, which warrants their separation, but I would not remove *Berthellina* any further than recognizing it as a separate genus. There are probably not more than four valid species of *Berthellina.*

The three genera in the Pleurobranchaeinae (*Pleurobranchaea, Euselenops, Pleurobranchella*) are well separated from each other by several characters. *Pleurobranchaea* has numerous species, many poorly defined (Marcus & Marcus, 1966). *Euselenops* is monotypic—*E. luniceps* (Cuvier, 1817) being widespread. The deepwater *Pleurobranchella* has possibly four species (Willan, 1977).

SYSTEMATICS

Berthellina Gardiner, 1936

Berthella Vayssière, 1896: 115 (*non Berthella* Blainville, 1825).

Berthellina Gardiner, 1936: 198. Type-species by original designation: *Berthellina engeli* Gardiner, 1936.

Definition

Relatively small pleurobranchs, body elliptical and convex; mantle large, smooth, simple and free all round, without an anterior crenulation; pedal gland never present; gill rachis smooth; anus at posterior end of gill membrane; shell beneath mantle, small (1/4–1/5 length of body), triangular or ovate, carried anteriorly, occasionally absent; teeth or radula elongate, lamelliform, serrated on distal section of posterior edge; mandibular elements cruciform on inner surface of jaw, smooth or indistinctly denticulate; vas deferens dilated into prostate gland; penis without accessory leaves.

Remarks

Species with these characters were attributed to *Berthella* Blainville, 1825 by Pilsbry (1896), Vayssière (1896, 1989) and Odhner (1926). Later authors used *Berthellina* for this genus (Gardiner, 1936; Odhner, 1939). The reasons for the change are given in the following summary.

Blainville (1825) created *Berthella* to include notaspidean opisthobranchs with lamellate teeth and smooth jaw elements; he designated *Berthella porosa* Blainville, 1825 as type-species. Vayssière (1898: 271) pointed out that *B. porosa* Blainville was a junior objective synonym of *Berthella plumula* (Montagu, 1803) and therefore Montagu's *Bulla plumula* took precedence as type-species. But a re-examination of the characters of *Berthella plumula* by Gardiner (1936) showed that this species has smooth, hook-like radular teeth and denticulate jaw elements. These characters had been applied to *Bouvieria* Vayssière, 1896, so *Bouvieria* became a synonym of *Berthella*. Gardiner (1936) created *Berthellina* for those species with lamellate radular teeth.

It is probable that some of the six species of *Berthellina* recognized by Burn (1962) are not valid. Indeed Edmunds & Thompson (1972) and Thompson (1976) amalgamated *B. engeli* with *B. citrina* (Rüppell & Leuckart), thus giving that species' distribution as Indo-Pacific, Mediterranean and marginally North Atlantic (e.g., Britain). Marcus & Marcus (1967a) named a new subspecies (*Berthellina engeli ilisima*), found from San Diego, California, to Guaymas, Mexico, but it was rejected soon afterwards (Bertsch, 1970). If *B. engeli* does exist in North America and is synonymous with *B. citrina*, then the one species would have an almost world-wide distribution. Care is needed here, and I concur with Thompson (1977) that hasty lumping of *Berthellina* species at this stage would be unwise. I think some reinstatements may be necessary in future (e.g. *Berthellina engeli* Gardiner). Marcus & Marcus (1957) transferred *Pleurobranchus (Oscanius) amarillius* Mattox to *Berthellina* where it is now considered a synonym of *Berthellina quadridens* (Mörch) (Burn, 1962; Marcus & Hughes, 1974; Thompson, 1977). One species overlooked in Burn's (1962) list is *Berthellina africana* Pruvot-Fol (1953) from the Atlantic coast of Morocco.

Abbott (1974) disrupted accepted nomenclature by replacing *Berthellina* with *Gymnotoplax* Pilsbry. But the type-species of *Gymnotoplax* (*Pleurobranchus americanus* Verrill) is undoubtedly a species of *Berthella*. Abbott's alteration is therefore unacceptable (Willan, 1978).

Berthellina citrina (Rüppell & Leuckart, 1828)
(Figs. 1–6, 9, 10, 13–19)

There are at least eight synonyms for this species. I do not give a synonymy here for three reasons. Burn (1962) has already presented an adequate synonymy and discussion; also the species is so widespread that a full synonymy would be very lengthy. Finally, in New Zealand this species has been confused with another pleurobranch (*Berthella mediatas* Burn) and references do not discriminate between the two.

Recent investigations have uncovered three more names to add to the synonymy of *Berthellina citrina*:

Pleurobranchus cuvieri Bergh, 1898: 129–131, pl. 11, figs. 19–27.

Berthella borneensis Bergh, 1905b: 69–70, pl. 5, fig. 3; pl. 11, figs. 45–47;

Berthella minor Bergh, 1905b: 70–71; pl. 13, figs. 1–3.

Marcus & Marcus (1970) redescribed *Berthellina cuvieri* (Bergh) from Madagascar, but their material easily falls within the range of variation of Indo-Pacific specimens of *B. citrina.* Narayanan (1970) studied material from the Gulf of Kutch, India, that he had pre-

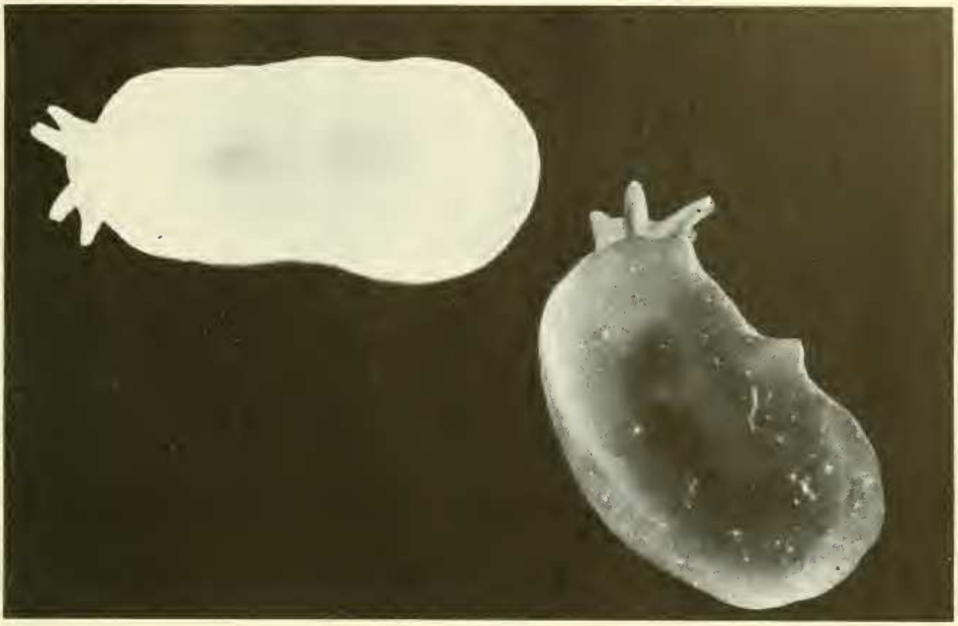


FIG. 5. *Berthellina citrina*. Lengths of both specimens approx. 40 mm. From 3–4 m, Leigh Harbour, North Auckland, 22 Nov. 1973. Photograph: G. W. Batt.

viously assigned to *Berthellina minor* (Narayanan, 1969) and placed that name also in the synonymy of *B. citrina*.

Live animal (Fig. 5)

During this study over 80 living specimens of *Berthellina citrina* have been examined; this is an adequate number to permit a description encompassing the natural variability of the species over its geographic range in New Zealand.

Shape elliptical, mantle wrapping entire upper part of body except rhinophores and oral veil which project anteriorly; rhinophores exposed from just behind their point of fusion; foot generally does not appear behind posterior edge of mantle when slug is crawling. Colour varies from deep apricot-orange to pale lemon; white spots almost always on surface, generally more numerous on sides and back, less apparent in largest individuals (approx. 50 mm long). Rhinophores and oral veil same colour as mantle surface. Mantle very delicate, smooth, soft, and translucent; anterior reddish-brown shell and posterior digestive gland, which appears as a black smudge, can be seen easily from dorsal aspect. When mantle margins are removed (e.g. through predation by *Pleurobranchaea maculata*), white spots become larger and more numerous after 5–6 days.

Rhinophores elongate, diverging by 50–60°, raised above oral veil, consisting of a spirally-wound sheet of tissue of 1½ whorls, open at last turn to leave a narrow lateral slit. Distal margin of rhinophoral sheet can be moved to control size of slit. At posterior-lateral corner, slit expanded to form a pyriform aperture, water enters along slit and is expelled through distal aperture. Eyes lie near, and just behind, basal aperture, covered by anterior edge of mantle.

Oral veil extending forward from head as a trapezoidal sail, anterior margin broad, wavy—but not nearly as sinuous as in *Berthella mediatas*; thickened lateral borders of oral veil have a deep furrow that expands into a cavity internally at base of veil.

Gill rachis smooth and cylindrical, basement membrane attaching gill to body for two-thirds of the gill's length; 18–28 pinnae on upper side of gill, first pinna always on upper side; mean number of pinnae for 15 specimens 23.7. Anus on dorsal side of gill, at hind end of basement membrane, opening on a slightly raised papilla; longitudinal folds in interior of rectum visible within anus. Prebranchial aperture opens just in front of, and slightly above, front of rachis; a much smaller aperture, the renal pore, opens below and behind base of rachis.

In specimens preserved in alcohol, mantle is creamish in colour. The delicate, translucent tissue becomes opaque, apparently thicker, and velvet-like, frequently obscuring shell.

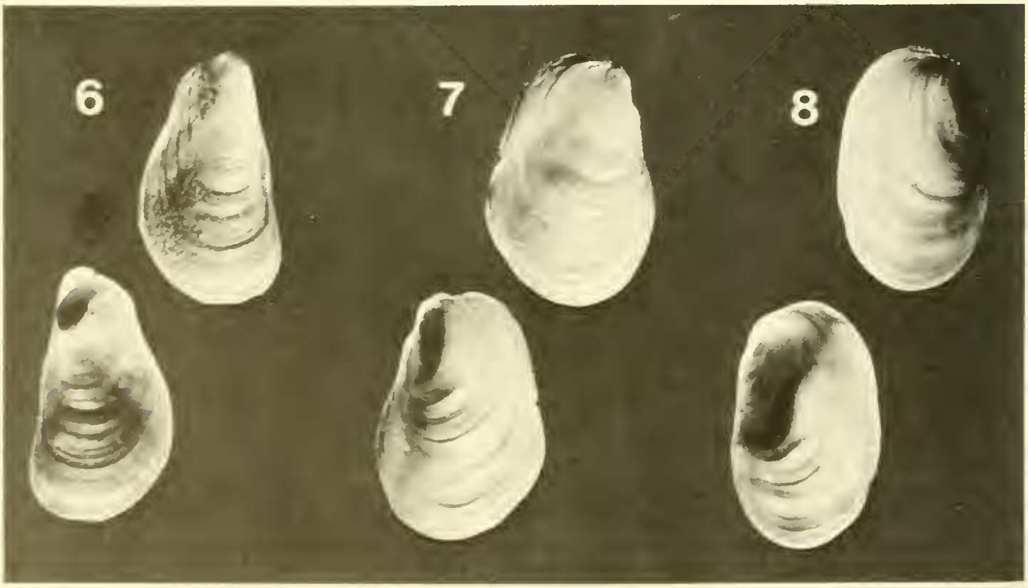
Shell (Figs. 6, 9, 10)

Shell small (1/4–1/5 length of extended body), thin, flattened, triangular; lying above pericardium in front of digestive gland; visible through mantle in living specimens. Consisting of two distinct, and clearly demarcated regions—protoconch of 1¼ to 1½ whorls and teleoconch; protoconch translucent, lacking regular sculpture but possessing some irregular calcification externally (Fig. 9); teleoconch spatulate, golden-brown or rich reddish-brown, older shells thicker and darker, clear apical region always present on teleoconch; first-formed teleoconch weakly convex and quadrangular, later growth unequal, producing eventually a triangular, spatulate form. Shell entirely covered by glistening, transparent periostracum that flakes off when shell dries; periostracum does not extend beyond shell margin.

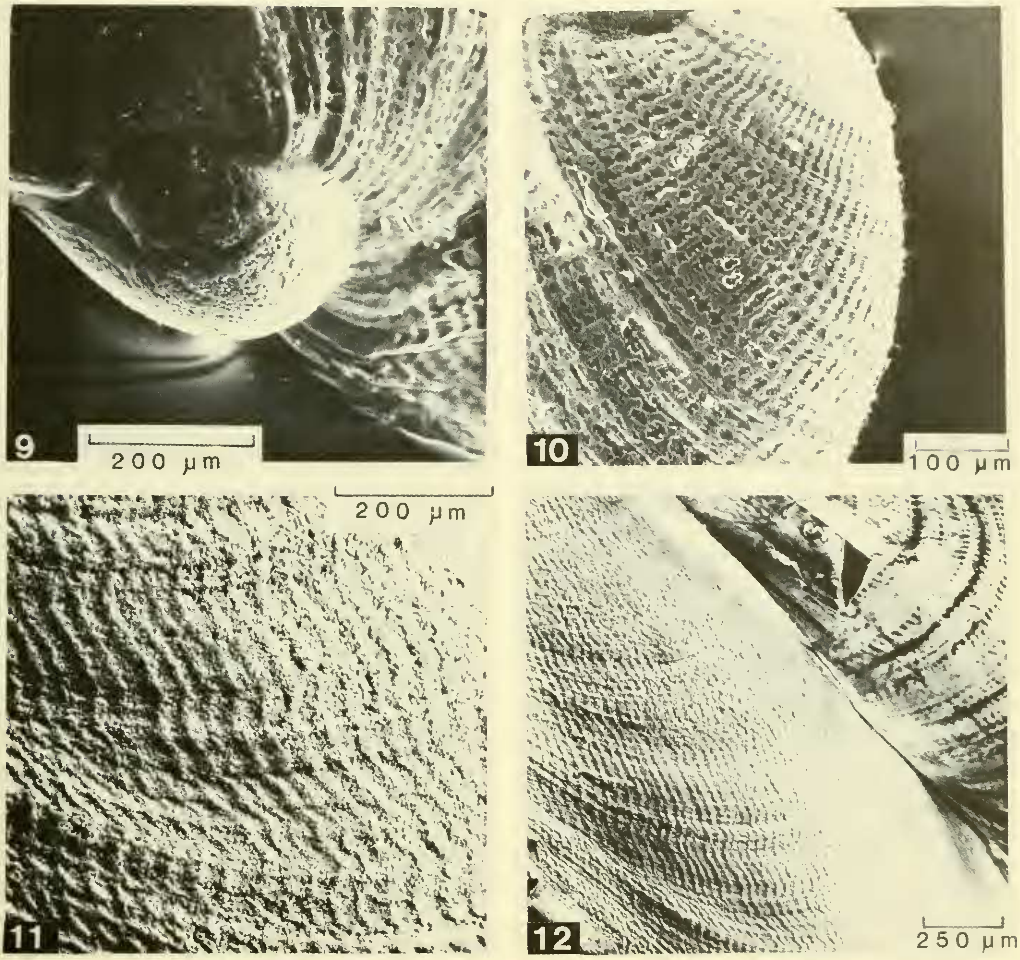
To the naked eye the surface sculpture is of irregular, concentric growth rings coalescing towards the margin in the adult shell to produce broad, flat ridges. Fine surface sculpture is most obvious near teleoconch apex (Fig. 10) and appears as a series of radiating, punctate depressions separated by flattened areas. Punctae occur in radial files, with some concentric organization; occasionally three to five merge within the radial rows. However, concentric fusion (which corresponds with growth checks) can also occur, becoming more obvious in older portion of shell, obliterating much of the regular radial organization.

All specimens of *Berthellina citrina* that I have examined (up to 5 cm) have had shells; this finding is contrary to that of Thompson (1970). He claimed that larger specimens (2 cm and over in extended body length) lacked shells. In New Zealand, *B. citrina* does not show the linear relationship between shell length and body length that has been shown for this species in the Red Sea (Gohar & Abul-Ela, 1957).

Five shells from specimens of *Berthellina citrina* taken at Leigh Harbour have been de-



FIGS. 6–8. Shells of New Zealand pleurobranchs. 6. *Berthellina citrina*. Length 6.1 mm × width 3.3 mm. Specimen from Pananehe Is., Spirits Bay, 14 Jan. 1972; 7. *Berthellina ornata*. 13.8 × 9.5 mm. Specimen from Army Bay, Whangaparoa Pen., 10 Jan. 1974; 8. *Berthella mediatas*. 10.3 × 6.4 mm. Specimen from Army Bay, Whangaparoa Pen., 10 Jan. 1974.



FIGS. 9–12. Scanning electron micrographs of shells. 9. *Berthellina citrina,* detail of protoconch. 10. *Berthellina citrina,* sculpture on apical region of teleoconch. 11. *Berthella ornata,* sculpture on exterior of teleoconch. 12. Same, periostracum has peeled off and appears at top right.

posited in the mollusc collection, Auckland Institute and Museum.

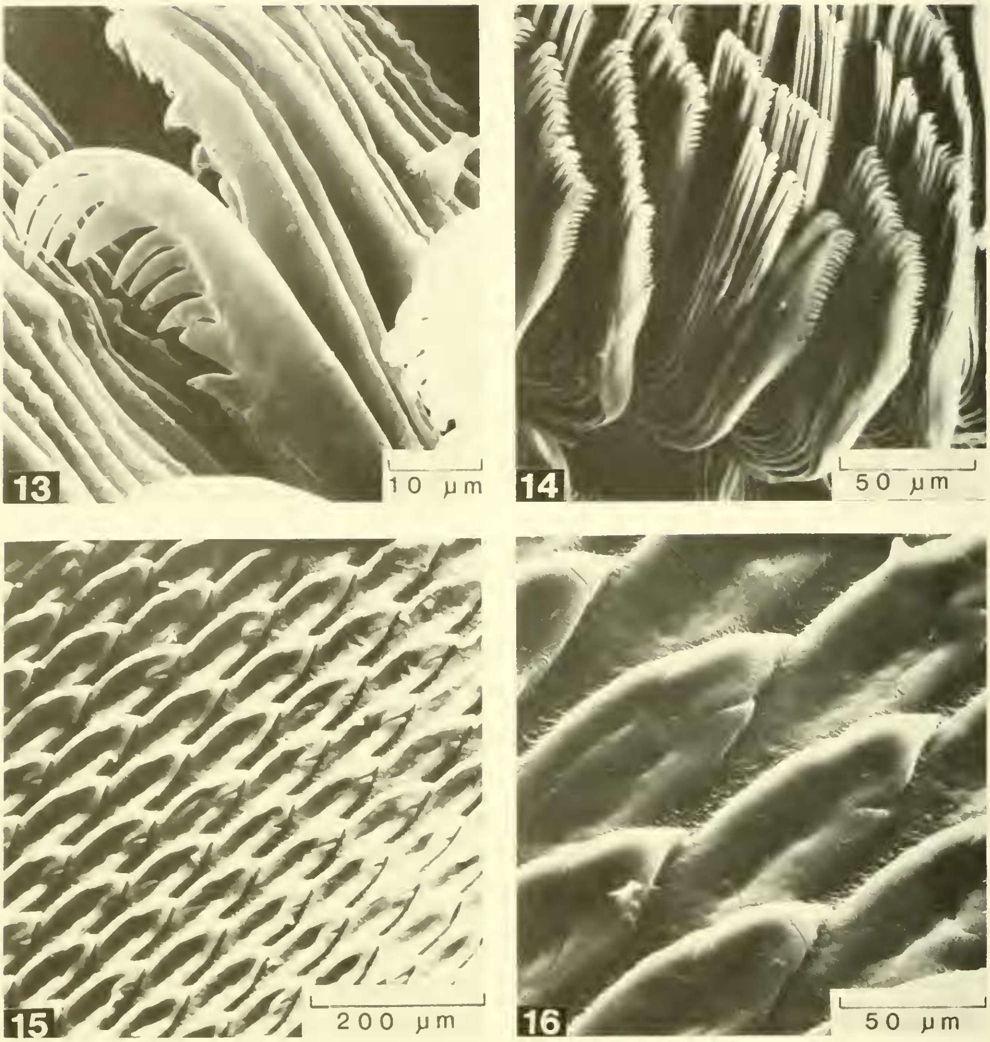
Radula (Figs. 13, 14)

Radula broad with two symmetrical halves, each forms one side of a V. The following radular description is applicable to an adult animal.

Central tooth lacking. Lateral teeth all similar, but showing gradual changes in length and denticulation across rows. Lateral teeth near midline 90 μm high, elongate, weakly denticulate on upper third of posterior face, terminal cusp differentiated from rest of tooth by a relatively deep groove. Base of each tooth curving sharply backwards and slightly thickened at its attachment to radular membrane.

Middle lateral teeth (Fig. 14) very large—140 μm high, comb-like, 15–20 strong denticles present on upper half of posterior face of blade; again terminal cusp longer than remaining denticles, all denticles project in same plane. There is a group of one to three broader denticles immediately below cusp; remaining denticles narrow, either needle-like or rounded, and frequently bifid at tips.

Outermost lateral teeth (Fig. 13) shorter (approx. 100 μm) than middle ones, and recurved towards posterior face; 15–20 denticles on upper half of posterior face, smaller



FIGS. 13–16. Radula and jaws of *Berthellina citrina*. 13. Detail of cusp and denticles on posterior face of a single tooth from middle lateral region of radula. 14. Outer lateral teeth and basal supporting structure within each row. 15. Mandibular elements on inner face of jaw. 16. Detail of same.

than those on middle teeth, with weaker grooves separating them, seldom bifid; terminal cusp projects in plane of tooth, tip slightly flexed upwards, and separated by a relatively deeper groove from rest of denticles, which project obliquely from posterior face, although still in same plane.

Examination of teeth with the SEM shows that the surfaces of the blade are smooth and there are no secondary structures on the denticles. There is a compression furrow on the shaft parallel to the anterior face. The furrow and the broad dorsal ridge beside it lock the blade in position laterally alongside adjacent teeth; there is thus a system for lateral support along the rows during the feeding movements.

Each tooth has an enlarged basal portion—a flange forming an oblique angle with the blade. On this flange, towards the base of the anterior face of the blade, is a raised ridge with a shallow depression at its base. A corresponding ridge on the next tooth in the same row fits into this depression, and into the depression on the flange of this tooth locks a ridge on the next tooth and so on. SEMs show the overlap of successive ridges down the row (Fig. 13).

Any single formula for *Berthellina citrina* would be inadequate since the number of rows and the number of teeth per row increase as the animal grows. Specimens examined had radular formulae in the range of 40 × 150.0.150 to 90 × 180.0.180. This is approximately the same as Burn's (1962) range (60 × 120.0.120 to 95 × 200.0.200).

Thompson (1970) published the first SEM photos of radular teeth of *Berthellina citrina*.

Jaws (Figs. 15, 16)

Two jaws, one on each side of the radula, are joined anteriorly at top and bottom by labial cuticle; anterior edges of cuticle recurved. Jaws rectangular, narrowing posteriorly to a point.

Jaws composed of columns of interlocked small elements; at jaw surface elements appear cruciform, with broad bases and elongate blades. Midway between base and blade are two rounded, lateral processes, one on either side; each process abuts against a similar process in the same row. "These processes are not exactly opposite, those on one side being slightly in advance of those on the opposite side, thus determining the slight obliquity of the rows. Toward the dorsal and ventral margins of the mandible, the elements become somewhat more irregular in form and depart from the typical shape found in the central areas." (MacFarland, 1966; part of description of *Berthellina engeli* Gardiner, but applicable to all species of *Berthellina*.)

A mid-ventral spike on flattened base of each element locks into place behind lateral processes of two adjacent elements so supporting them from behind; overlapping tip of blade of element in the next row posteriorly acts to enforce connection from above. Blade of one element fits between base and lateral processes of two adjacent elements; raised and with dorsal flange so that dorsal surface presents only a series of similar flattened blades. SEM photos (Figs. 15, 16) give a view of this top surface.

Mandibular elements are approx. 80 μm long and up to 30 μm wide at centre of jaws, base slightly narrower; element widens in a smooth curve to blunt tips of lateral processes, element constricts just above lateral processes and broadens anteriorly to form blade. Blade elongate, straight-sided, narrowing gradually to a pointed tip.

All jaws but one had no denticulation on the blade. The specimen in Figs. 15 and 16 had one or two definite denticles developed near the apex of many of the mandibular elements. Most had a single cusp, but a few showed a weaker cusp in a similar position on the other side of the blade. These weaker cusps lay in the plane of the mandibular elements and did not break the smooth outlines of the blade. They were not separated at their bases from the rest of the dorsal surface of the element and narrowed rapidly. Baba (1937) and Burn (1962) have also noticed these structures on the mandibular elements of *Berthellina citrina*.

The presence of these rudimentary and irregular cusps on the mandibular elements of *Berthellina citrina* invalidates, in a sense, the diagnostic character of smooth-sided jaw elements for the genus; but they are so different from those of *Berthella* and *Pleurobranchus* that the mandibular elements are still an important taxonomic character.

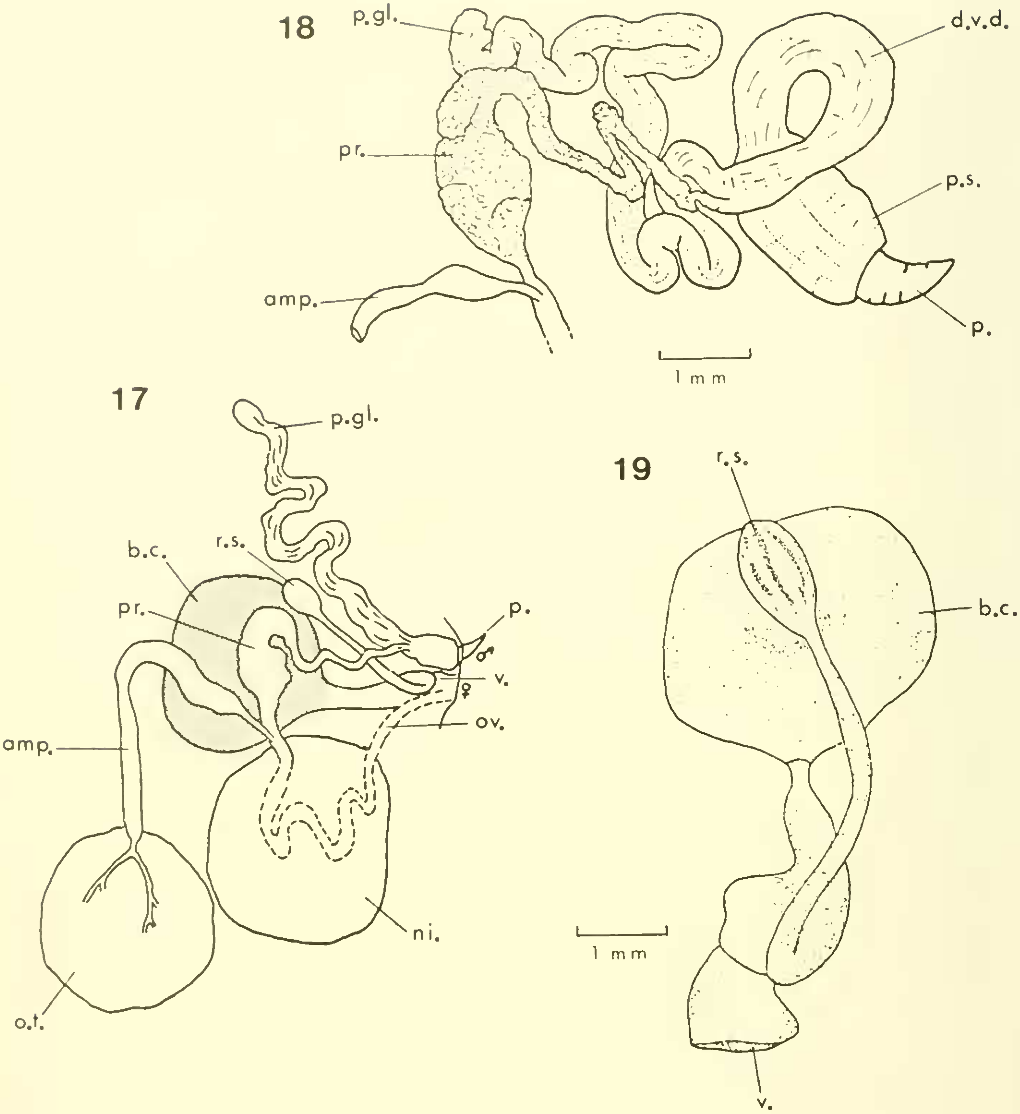
Reproductive system (Figs. 17–19)

Reproductive apertures located on right side just in front of anterior end of gill, surrounded by a low, collar-like ridge. Most preserved specimens examined had terminal portions of the reproductive ducts everted to some degree. Penial opening foremost, middle opening marks vagina, and behind that is large aperture of oviduct. When genital papilla is everted, oviduct and vagina are separated by a broad flap of tissue projecting upwards from surrounding collar, but in retracted state they share a common atrium.

Ovotestis yellowish, large, lying against right side of digestive gland, appearing glandular because of layers of immature eggs. Hermaphrodite duct divides into two as it enters ovotestis; each branch fine, white; after a short distance each divides repeatedly.

Upon leaving ovotestis, hermaphrodite duct enlarges into an ampullar region which crosses beneath looped intestine and rises to dorsal surface of visceral mass where it appears as a prominent tube, passing anteriorly across fluffy, yellow mucous gland. At anterior end of mucous gland, hermaphrodite duct constricts and forms a T-junction with a larger duct, anterior limb of the latter being proximal vas deferens; posterior limb enters nidamental gland complex after a very short distance.

Proximal vas deferens short, rapidly enlarging to yellow prostate gland; distal vas



FIGS. 17–19. Reproductive system of *Berthellina citrina*. 17. Composite view of structure of the reproductive organs. 18. Detail of structures associated with distal section of vas deferens and penis. 19. Detail of seminal receptacles in a mature animal. Abbreviations: amp. = ampulla; b.c. = bursa copulatraix; d.v.d. = distal section of vas deferens; ni. = nidamental glands; o.t. = ovotestis; ov. = oviduct; p. = penis; p.gl. = penial gland; pr. = prostate gland; p.s. = penial sheath; r.s. = receptaculum seminis; v. = vagina.

deferens much narrower, undergoing several loops and enters base of penis; a larger, much-coiled penial gland located there too (penial gland has also been called accessory prostate gland—Vayssière, 1898, MacFarland, 1966); penial gland elongate, thick-walled with longitudinal ridges, coiled about distal vas deferens, blind-ending. Beyond entrance of penial gland vas deferens is tightly looped several times at base of penis. Penis short and curved, unarmed, projecting forward when everted, surrounded by stout muscular sheath. When everted, penis has weak concentric ridges on its surface and ends in a sharp tip. Fig. 18 gives a diagram of the anterior organs of the male section of the pallial gonoduct.

Two prominent sacs open into vagina—

bursa copulatrix which is spherical and thin-walled, and receptaculum seminis, which is smaller and thick-walled. Receptaculum seminis has a terminal, club-shaped dilation and a curved canal looping to enter vagina near its opening, where another swelling is present (see Fig. 19). No connection of vagina with oviduct exists, save through the external vaginal opening into its common exit close to the nidamental gland complex.

Distribution

The geographic range of *Berthellina citrina* in New Zealand is entirely northern (Aupourian). It extends down the east coast of the North Island, from Northland to the Bay of Plenty. There are no records so far of its occurrence on the west coast (see Appendix).

Elsewhere *Berthellina citrina* has been recorded under various names from Australia (Quoy & Gaimard, 1832; O'Donoghue, 1924; Dakin, 1952; Burn, 1962; Thompson, 1970), New Caledonia (Risbec, 1928), Hawaii (Kay, 1979), Palau Islands (Marcus, 1965), Japan (Baba, 1937, 1949, 1969; Hirase, 1937; Usuki, 1969), Sri Lanka (Kelaart, 1883), South Africa (Macnae, 1962), Indonesia and Mauritius (Macnae, 1962; Marcus & Marcus, 1967a), Gulf of Kutch, India (Narayanan, 1970), Gulf of Elat (Marbach & Tsurnamal, 1973), and Red Sea (Gohar & Abul-Ela, 1957). Apart from *B. oblongata* (Audouin) and *B. saidensis* (O'Donoghue) from the Red Sea, *B. citrina* is the only species in this genus known in the Indo-Pacific (Burn, 1962).

I can confirm Burn's (1962) and Thompson's (1970) records of *Berthellina citrina* from New South Wales because I have collected specimens there myself. I have also collected *B. citrina* in southern Queensland and Vanuatu (New Hebrides). Dr. M. C. Miler found this same species in the Solomon Islands during the Royal Society B.S.I.P. Expedition of 1965.

Discussion

The identity of *Berthellina citrina* in New Zealand cannot be doubted. In *B. citrina* the combination of a small, spatulate shell, elongate radular teeth with denticulate posterior edges, mandibular elements with smooth (or weakly denticulate) blades, and prostatic dilation of the vas deferens are thoroughly distinctive features allowing easy identification and separation from all other New Zealand pleurobranchs.

Biologists, following Bergh (1900), have applied the name "*Bouvieria aurantiaca* (Risso)" indiscriminately to any yellow or orange pleurobranch from New Zealand that lacked the dorsal, spotted pattern of *Berthella ornata,* so the two species answering this description (*Berthellina citrina* and *Berthella mediatas*) have not been hitherto distinguished. Table 2 lists the major characters which separate these two species. The only "*B. aurantiaca*" in the New Zealand literature that can be identified as *Berthellina citrina* is that by Morton & Miller (1968). This is because these authors give an excellent colored illustration of a living animal (pl. 11, fig. 6). The inclusion of *B. citrina* by Gordon & Ballantine (1977, in Appendix 3), was on my advice. "*Bouvieria aurantiaca* (Risso)" auct. is a valid species of *Berthella* from the Mediterranean Sea, and from the available literature it would appear close to *Berthella mediatas* Burn.

Several recent publications have treated the biology of *Berthellina citrina*. A summary of development was presented by Gohar & Abul-Ela (1957). Usuki (1969) studied reproduction, development and life history of Japanese specimens. Marbach & Tsurnamal (1973) made observations on feeding and acid secretion of specimens from the Gulf of Elat (Red Sea).

I have not included any distribution records for *Berthellina engeli* Gardiner in the geographic range list given above because I feel that it is premature to synonymize that species with *B. citrina*. In specimens of *B. engeli* that I have examined, the shells have been consistently more oval in shape, proportionately larger and positioned more posteriorly on the visceral mass.

Berthella Blainville, 1825

Berthella Blainville, 1825: 370. Type-species by original designation: *Berthella porosa* Blainville, 1825 (= *Bulla plumula* Montagu, 1803).

Cleanthus "Leach MS., 1819" Gray, 1847: 163. Published in the synonymy of *Berthella* Blainville, 1825.

Bouvieria Vayssière, 1896: 66. Type-species by subsequent designation (Odhner, 1926: 22): *Pleurobranchus aurantiacus* Risso, 1818.

Gymnotoplax Pilsbry, 1896: 20. Type-species by subsequent designation (Willan, 1978:

339): *Pleurobranchus americanus* Verrill, 1885.

Berthellinops Burn, 1962: 135. Type-species by original designation: *Berthellinops serenitas* Burn, 1962.

Abbott (1974) placed *Cleanthus* Gray as a synonym of *Pleurobranchus* Cuvier, 1804. Elsewhere (Willlan, 1978) I have already shown that the holotype of *Pleurobranchus americanus* Verrill, upon which *Gymnotoplax* Pilsbry is based, is a typical *Berthella*. Apart from a supposedly opposite (instead of alternate) arrangement of pinnae on the gill, *Berthellinops* Burn is a *Berthella*. Burn himself later examined additional material and found this arrangement not to persist, and accordingly would now treat *Berthellinops* as a synonym of *Berthella* (R. Burn, personal communication, July 1977).

Definition

Shelled pleurobranchs; body elliptical and convex; mantle large, simple and free, without an anterior indentation; pedal gland present; shell ovate, large (at least half length of body); gill rachis smooth or weakly tuberculate; radula with simple, curved or erect teeth; mandibular elements with smooth or denticulate blades; reproductive system lacking prostate gland.

Remarks

Members of the genus approach *Berthellina* in their relatively small size and (generally) smooth gill rachis; but in characters of the radula, jaws and reproductive system they appear to show close affinities with *Pleurobranchus*.

Two *Berthella* species are found in New Zealand; both range throughout the country. There is the endemic *Berthella ornata* (Cheeseman), and secondly *Berthella mediatas* Burn, a species shared with temperate southern Australia.

Berthella ornata (Cheeseman, 1878)
(Figs. 7, 11, 12, 20–31)

1879. *Pleurobranchus ornatus* Cheeseman: 175, pl. 15, figs. 1, 2.—1879, Cheeseman: 378, pl. 16, figs. 1, 2.—1880, Hutton: 124.—1896, Pilsbry: 206, pl. 47, figs. 22, 23.—1898, Vayssière: 337, pl. 14, figs. 18, 19.—1913, Suter: 550 (in subgenus *Berthella* Blainville).—1915, Suter: pl. 77, fig. 6.

1924. *Bouvieria ornata* Cheeseman; Odhner: 51, 86.—1926. Odhner: 22.—1937. Powell: 89, No. 1404.—1953, Milligan: 134, 1139.—1957, Powell: 114.—1961, Powell: 107.—1964, Williams: 19, illust.—1968, Morton & Miller: 167, 576, pl. 11, fig. 7.—1976, Powell: 112.—1977, Gordon & Ballantine: 112.—1979, Powell: 282, pl. 51, fig. 3.

The description of *Pleurobranchus ornatus* Cheeseman (and *Pleurobranchaea novaezealandiae* Cheeseman) first appeared in *Proceedings of the Zoological Society of London* for the year 1878. An identical description was printed in the Transactions and Proceedings of the New Zealand Institute for the same year (but not published until 1879) (Pilsbry, 1896). Cheeseman's descriptions were each accompanied by a figure, meticulously drawn by his sister Evelyn (A. W. B. Powell, personal communication, 1977). Powell (1939b) designated these drawings as iconotypes and he has recently republished them in colour (Powell, 1979). These iconotypes are held in the Malacology Department, Auckland Institute and Museum.

Live animal (Figs. 20, 21)

Body oval to elongate; mantle smooth and soft, broad and circular. In actively crawling specimens (Fig. 22a) rhinophores and oral veil project beyond front edge of mantle, mantle margin just covers point of fusion of rhinophores; sole of foot often visible posteriorly. Mantle covers body as a broad cloak, lateral areas extend beyond foot to sweep the ground. In resting animals, tail and oral veil tuck beneath mantle, and rhinophores barely show (Fig. 22b).

Anterior edge of mantle truncate, raised in midline to allow outward extension of rhinophores, but not indented mid-anteriorly; posterior edge of mantle broadly rounded. Mantle thick in central area, thinner towards margins, not delicately translucent as in *Berthellina citrina*; margin entire, but often sinuous—particularly on right side where upthrown posterior-lateral edge forms a temporary exit for exhalant water current. Most animals have an apparently smooth mantle surface, but in some, large pores can be detected by eye on the surface. When an animal is removed from its substrate, the broad lateral areas of the mantle bend round the foot and hug the sides

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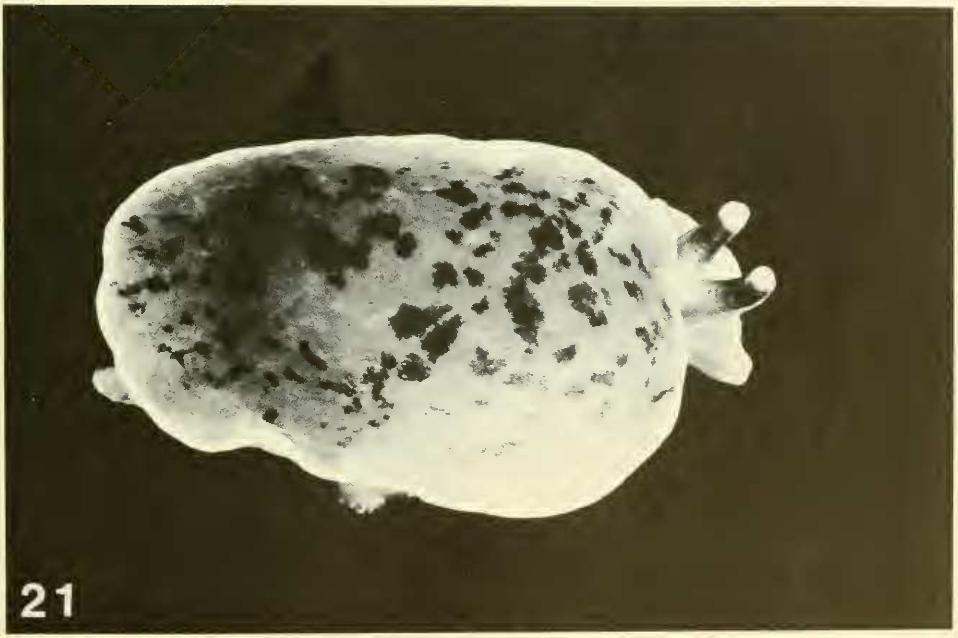

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FIGS. 20, 21. *Berthella ornata*. 20. Length = 40 mm. From intertidal reef platform to left of Matheson Bay, near Leigh, North Auckland, 5 Oct. 1975. Photograph: R. C. Willan. 21. Length = 38 mm. From Pacific Bay, Tutukata, Northland, 8 March 1974. Photograph: G. W. Batt.

of the body to give a cylindrical and protective form.

Colour characteristic, consisting of an even ground shading from pure white to pale (or rich) reddish-brown to orange-brown. Overlying this are irregular blotches and spots, all a rich, dark, red-brown and very variable in shape and size. Some individuals show few (approx. 30) markings over mantle, more often entire mantle is covered. Markings tend to be largest and more concentrated on mid-dorsal region of mantle (area over shell and digestive gland), they decrease in size and number outward from the centre, and are small and scattered on anterior and lateral marginal areas. In some animals, particularly small ones (up to 10 mm in extended length), these spots extend out to mantle margins; adults have a more or less broad zone next to mantle margin that possesses nothing but background coloration; margin itself is opaque white. Digestive gland appears as a dark central smudge; shell not visible through mantle.

When the animal is handled roughly and repeatedly, or when the mantle is prodded, the mantle produces a thick, milky-white repugnatory fluid; discharge can be localized or occur over the entire surface; secretion becomes incorporated with clear body mucus and is left behind as slug crawls away.

Foot large, oval, broad-soled, truncated in front and rounded behind; border minutely crenulate all round but crenulations are weakest at anterior margin; sole sticky. The posterior quarter of sole in fully grown specimens has a large, but indistinct, circular pedal gland. All specimens examined had a creamy-white foot, with a thin, opaque white line at margin. No markings present on the foot sole, but lightly-pigmented blotches sometimes present on dorsal surface near tail.

Oral veil broad, with thickened, moderately pronounced edges that are grooved laterally; anterior border sinuous, but not nearly as deeply embayed as in *Berthella mediatas*; very weakly crenulate along anterior margin. Oral veil creamy-white, always without markings, though an indistinct white line along anterior border is present. Undersurface (in mid-anterior region) and lateral edges periodically touch the substratum in an exploratory manner as animal crawls.

Rhinophores Y-shaped, joined at bases and diverging by 30–45°; raised upwards at 90° from horizontal in an actively crawling animal, and at 45–60° when animal quiescent; each limb can be moved independently. Tips of rhinophores always white; in live specimens tips are active and mobile; very flexible as they move to test oncoming water. There is some degree of variability in coloration of lower regions of rhinophores; these regions are often the same colour as mantle. Specimens with darkly-pigmented mantles usually have dark, reddish-brown or chocolate pigment in this region; extreme tips and fused basal areas are unpigmented. Small specimens (and adults with pale dorsal coloration) have rhinophores lightly pigmented with buff-brown or cream. Coloration of rhinophores changes to some extent with size of the individual. Most small specimens (less than 20 mm extended length) had cream rhinophores (e.g. nine from Goat Island Bay, Leigh; May 1974). Larger specimens (greater than 30 mm extended length frequently had rhinophores bearing darker pigmentation (e.g. 10 from Waiwera; January, July, September 1974). In living specimens rhinophores appear smooth externally, but in the preserved state strong contraction of these organs produces deep transverse grooves.

When magnified, both oral veil and rhinophores are seen to be covered with white, conical papillae. These papillae are evenly distributed over oral veil and are very dense towards tips of rhinophores. Sparse, white papillae are also present on mantle and tail.

Berthella ornata has an exceptionally long gill, reaching backwards almost to level of tip of tail; gill attached to body wall for over half its length by basement membrane. Number of pinnae ranges from 18–25, first pinna always arises on upper side of rachis; mean number of pinnae counted on 12 adults—22; approximately half the pinnae arise from posterior free end of gill. Pinnules are particularly large and give the gill a feather-like appearance. All specimens examined had creamy-white gills, devoid of markings.

In living, and some well-fixed specimens, it is possible to see that the rachis is not smooth, but regularly covered with weak ridges or knobs where the pinnae join. These ridges continue on to the surface of the pinnae which appear smooth. It would seem that these weak knobs are homologous with the better-developed tubercles of *Pleurobranchus* Cuvier. Most preserved *B. ornata* appear to have smooth rachises to their gills.

Anus opens at side of body, on dorsal side of gill at hind end of basement membrane (i.e.

about half-way along gill's total length); anus opens on a low, conical, backward-projecting papilla.

Numerous glassy spicules (Fig. 23) are embedded in mantle, particularly at base of rhinophores where limbs diverge; spicules are 50–75 μm in greatest total length; spicules consist of 2, 3, or 5 separate rays, each is straight or slightly curved, and terminates in a blunt tip, nearly all rays are equal in length. Although rays of spicules project in all directions they do not diverge at right angles. Spicules very brittle, contraction of animal on death is enough to shatter most of then. Spicules effervesce in dilute acid suggesting they are, like the shell, calcareous.

Shell (Fig. 7)

Shell always present, generally rectangular and flattened, sides constricted towards apical (posterior) part; slightly convex with anterior and posterior margins elevated from horizontal. Protoconch of 1½ whorls, on left posterior-lateral corner; posterior flange of shell higher than level of protoconch. Lateral margins of shell parallel, or showing a slight divergence anteriorly; anterior margin broadly rounded. Macroscopic sculpture is of irregular concentric folds, flattened, narrow and compressed towards margins. Microsculpture (Figs. 10, 11) consists of numerous, radiating ridges interspersed with broad depressions; ridges and depressions are parallel, directed in wavy lines that cross concentric folds; surface granular in texture. This sculpture is present only towards shell apex and becomes progressively weaker until, over the anterior third of teleoconch, it is obsolete.

Outer surface of shell covered with a thin, iridescent periostracum (Fig. 12) which readily peels off; it is dull, whitish and chalky on shells of preserved specimens; periostracum does not exactly duplicate underlying wavy sculpture of shell, but appears punctate towards apex and smooth anteriorly.

Shell thin, white towards apex, pale buff over remainder; interior brownish-orange towards anterior edge, with a faint, red-brown streak towards left corner. Interior sculptured with raised, concentric ridges that narrow towards anterior margin.

Four shells from specimens of *B. ornata* taken at Mahurangi Island, off Waiwera Beach, have been deposited in the mollusc collection, Auckland Institute and Museum.

Radula (Figs. 24, 28, 29)

Pale yellow-brown, broad and rectangular; maximum length 7.0 mm, width 4.0 mm when flattened. No rachidian in any row. Lateral teeth small and simple; inner and middle laterals (Fig. 28) 40–60 μm high, hook-like, curved, with sharp-pointed apices; all have a relatively broad blade, both edges of which are smooth. Outer lateral teeth erect, straight-sided, with relatively narrow blades and rounded apices; outermost lateral teeth decrease regularly from 45 μm to 30 μm (for extreme outer lateral tooth). There are many rows of teeth in the radula, giving the following range of radular formulae for adult specimens: 90 × 65.0.65 to 140 × 140.0.140. These formulae are high compared to those of other *Berthella* species.

Jaws (Figs. 30, 31)

Relatively small (approx. 2.0 mm long in adults), oval, with both ends rounded; jaws composed of numerous, cruciform, and relatively squat elements, each being 60–65 μm long. Jaw elements broad-based, bases concave, widening to lateral processes; sides of blade smooth; each element terminates at a blunt, pointed apex (Figs. 30, 31); very rarely some elements have a weak denticle on side of blade about half way between a lateral process and apex. Apical thickenings on all mandibular elements are very apparent in both light microscopical views and SEM photos; thickenings rise from plane of top surface of element (i.e. that on inner surface of the jaw) and terminate in a sharp cusp; edges of blade near apex can also be raised. Such terminal thickenings have not been previously recorded for pleurobranch mandibular elements. The jaw elements of *Berthella ornata* are broader and squatter than those of *Berthellina citrina*.

Reproductive system (Figs. 25–27)

Similar to that of *Berthellina citrina*, but with no prostatic enlargement of the vas deferens. The reproductive system of *B. ornata* differs in several other points from that of *B. citrina*, and these details are reported because of their specific importance.

Although size of nidamental glands varies with age and maturity, two regions are discernible. A dorsal, white and compact albu-

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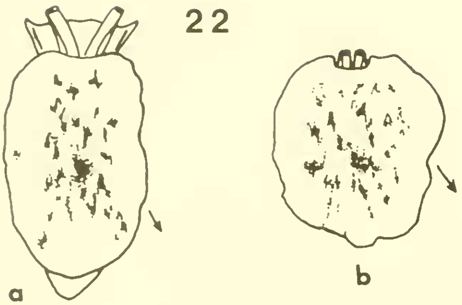

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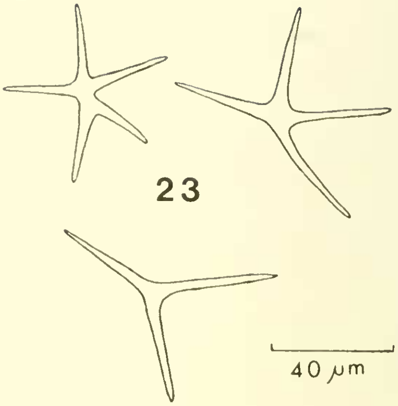

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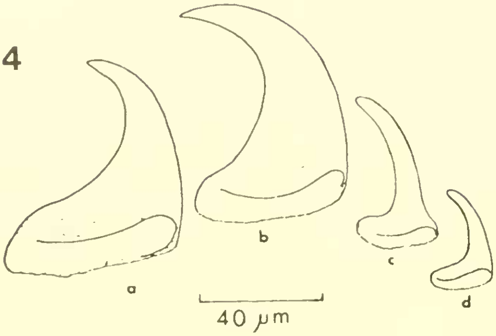

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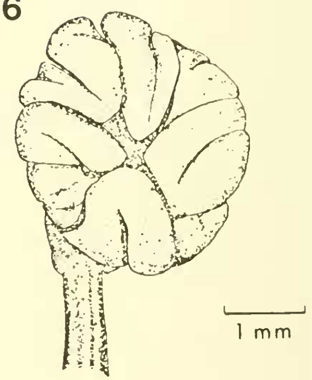

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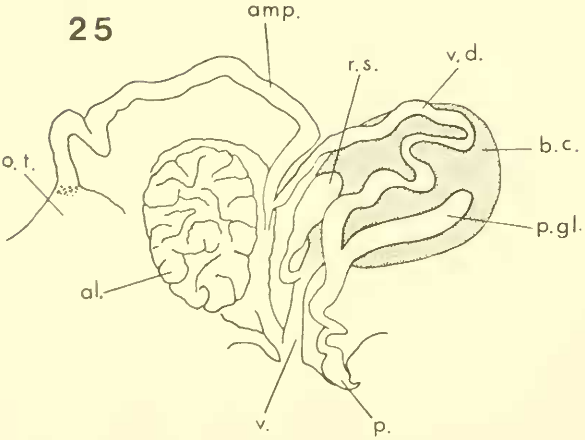

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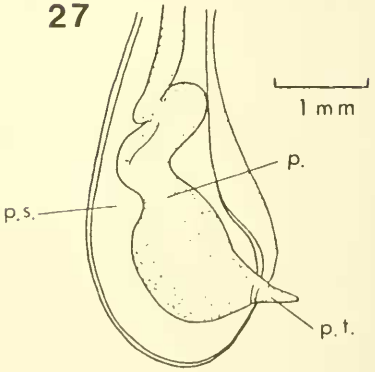
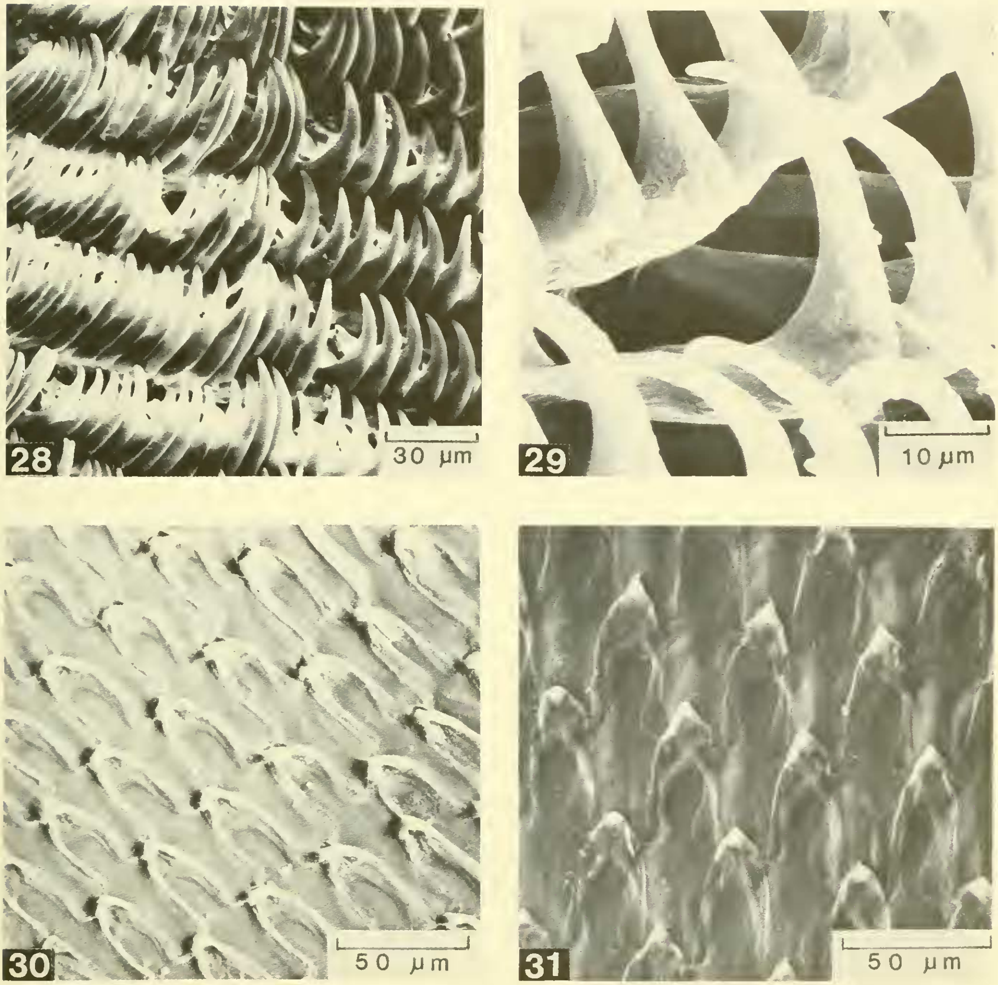


FIGS. 22–27. *Berthella ornata*. 22. Whole animal from above, a = crawling, b = resting. Arrow indicates direction of exhalant current; 23. Spicules from mantle; 24. Radular teeth, a = inner lateral, b = middle lateral, c = outer lateral, d = outermost lateral; 25. Composite view of structure of reproductive organs; 26. Detail of albumen gland from ventral surface; 27. Detail of penis and penial sheath, the latter cut open. Abbreviations: al. = albumen gland; amp. = ampulla; b.c. = bursa copulatrix; o.t. = ovotestis; p. = penis; p.gl. = penial gland; p.s. = penial sheath; p.t. = apex of penis; r.s. = receptaculum seminis; v. = vagina; v.d. = vas deferens.



FIGS. 28–31. Radula and jaws of *Berthella ornata*. 28. Inner and middle lateral teeth showing change in structure across a row. 29. Detail of a single middle lateral tooth. 30. Mandibular elements on inner face of jaw. 31. Detail of the same.

men gland (Fig. 26), consisting of a tightly-coiled tubular mass that is convoluted in external apperance, and the mucous gland. This latter gland lies below the albumen gland; it is flattened, solid and cream in color.

The vagina is grooved internally and passes as a long, straight canal to two seminal receptacles; vagina opens directly into a large sac-like bursa copulatrix whose dark-colored contents can be seen through the thin wall. A side branch arises from vaginal duct just before base of bursa copulatrix and loops to smaller receptaculum seminis. This concentration is well back from vaginal aperture. There is a dilation in front of receptaculum seminis; receptaculum solid, roughly conical in shape, pressed against bursa copulatrix when in its natural position.

Vas deferens much-convoluted, thin-walled, of a slightly larger diameter than hermaphrodite duct, pressed against membrane surrounding bursa; vas deferens lacks a prostatic glandular region. A penial gland arises from vas deferens at level of bursa; it is finger-like, flattened, thin-walled, not extensively coiled. Penial gland pressed against membrane of bursa copulatrix, although not entwined with vas deferens. Beyond junction with penial gland, vas deferens runs beneath vagina, both lie within a common membranous sheath. Penis unarmed, of a smaller diameter than hermaphrodite duct; when retracted, penis remains coiled inside its sheath.

Distribution

Berthella ornata is found in clean, rocky situations on open or partially sheltered coasts throughout New Zealand. It ranges from the intertidal to shallow subtidal depths (approx. 15 m).

Discussion

A distinctive species of pleurobranch, *Berthella ornata* is the only endemic shallow-water New Zealand member of the order Notaspidea. It can be distinguished from its New Zealand congener, *B. mediatas* Burn, by colour, texture of mantle surface, gill length, and position of anus. *B. ornata* has smooth-bladed mandibular elements and relatively large, curved, middle lateral radular teeth; *B. mediatas* has strongly denticulate blades to the mandibular elements and relatively small, less curved, middle lateral teeth.

Berthella ornata has several other characteristics important from a taxonomic view and which may prove significant in future studies of phylogeny within the genus: mantle coloration; gill; mandibular elements; radula; reproductive system.

Other than *Berthella ornata,* few members of the genus have distinctive colour patterns on the mantle. Most species are uniformly dull yellow-orange or pale fawn, the mantle being more or less translucent with the dark digestive gland and light ovotestis showing through. A literature search revealed five other *Berthella* species with conspicuous darker markings on the mantle surface:

Berthella ocellata (Delle-Chiaje, 1828) from the Mediterranean Sea. This species has a yellow-ochre to reddish-brown ground colour overlain with large, white or yellowish blotches; it has a much narrower shell than *B. ornata,* with a tall, projecting spire.

Berthella stellata (Risso, 1826) from the Mediterranean Sea. It has numerous, small spots on a bright yellow background; there is an unpigmented central area in the form of a cross. *B. stellata* has denticles on the blades of the mandibular elements.

Berthella scutata (Martens, 1880) from Mauritius. This species is yellowish with large spots of dark purple-brown on the mantle and a few smaller spots on the oral veil, rhinophores and sides of the foot; the mantle is evenly and finely granulose all over; like the previous species, *B. scutata* has denticulate mandibular elements. *B. scutata* may be a species of *Pleurobranchus*; Marcus (1977) considers it a *nomen dubium.*

Berthella kaniae Sphon, 1972 from Panama and Mexico. Ground colour is deep yellow (Thompson, 1970). It has a whitish or pale fawn mantle, patterned over the entire surface with minute, pale brown, polygonal markings; this species has two short denticles on either side of the blade of each mandibular element.

Berthella kaniae Sphon, 1972 from Panama and Mexico. Ground colour is deep yellow to almost white; the mantle, gill, and veil, as well as the tips of the rhinophores and the area around the genital apertures are spotted reddish-brown. Like *B. ornata*, it has smooth blades to the mandibular elements, but in *B. kaniae* the teeth are of similar size and shape across each row of the radula, and the living animal has the capacity to autotomize parts of the mantle edge (Sphon, 1972)—a behaviour never observed in *B. ornata.*

Two of the smaller *Pleurobranchus* species also have darker markings on the mantle—*Pleurobranchus tessellatus* Pease, 1868 from Polynesia, and *P. ovalis* Pease, 1868 from Tahiti and Australia.

In *Berthella ornata* the gill plume is particularly long, extending for more than half the body length, the rachis is not smooth but weakly knobbed where a pinna branches off. These knobs appear homologous with the rachal tubercles of *Pleurobranchus s.s.* Further detailed studies must be made of the gills of *Berthella* and *Pleurobranchus* to see if a separation based on this single characteristic is as clear as has previously been assumed.

Both Burn (1962) and Thompson (1970) diagnose *Berthella* as having denticles on the blades of the mandibular elements. Yet there are none in *B. ornata.* A small group of other *Berthella* species has also been reported to have smooth-edged elements; these are: *B. ocellata* (Delle-Chiaje) (Vayssière, 1898: 288); *B. kaniae* Sphon; *B. tupala* Marcus (Bertsch, 1975).

Berthella mediatas Burn, 1962
(Figs. 8, 32–44)

1900. *Pleurobranchus aurantiacus* Risso; Bergh: 210, pl. 20, figs. 34–38 (*non Pleurobranchus aurantiacus* Risso, 1818).
1924. *Bouvieria (Pleurobranchus) aurantiaca* (Risso); Odhner: 51.—1939a, Powell: 217, No. 1232 (*non Pleurobranchus aurantiacus* Risso, 1818).
1955. *Bouvieria aurantiaca* (Risso); Powell: 118 (*non Pleurobranchus aurantiacus* Risso, 1818).
1957. *Pleurobranchus punctatus* Quoy & Gaimard; Burn: 15 (*non Pleurobranchus punctatus* Quoy & Gaimard, 1832).
1962. *Berthella mediatas* Burn: 142.—1966b, Burn: 271, No. 26.—1969, Burn: 80, No. 15 (listed as "*Berthella mediata* Burn (1962)").

Live animal (Fig. 32)

Extended body length to 30 mm. Mantle broad, with lateral margins extending beyond sides of foot; when animal is crawling, foot exceeds mantle in length; rhinophores and oral veil project well in advance of raised anterior margin. Mantle relatively thick, dull cream or pale brownish-orange, with a slight central darkening due to the underlying digestive gland; occasionally a few small, diffuse, white spots are present as well; shell not usually visible. Mantle highly porous, pores large and very numerous over entire surface, visible in strong light without magnification. Glassy spicules similar to those of *B. ornata* are present amongst pores on mantle but require magnification to be seen. Foot hidden all round by mantle except posteriorly; dirty yellow-orange in color and unspotted; anterior mucous groove makes front border darker; pedal gland present on sole, positioned towards one side, appears as a darker, thickened, triangular region, with base at back of foot.

Oral veil large, narrow at insertion and broadening towards anterior border; tips of grooved lateral areas noticeably forward-projecting. Anterior margin deeply sinuous, with a mid-anterior embayment. Oral veil pale, dirty yellow, lateral areas darker.

Rhinophores long, projecting well beyond mantle's anterior border; pale yellow or orange.

Gill relatively small, never extending behind tail when the animal is crawling, always covered by mantle, attached for half its length to body wall, rachis narrow, smooth; 18–23 pinnae arise from upper surface and alternate

FIG. 32. *Berthella mediatas*. Length = 17 mm. From Cape Egmont, Taranaki, 16 July 1974. Photograph: G. W. Batt.

with a similar number below; pinnae bear smaller pinnules (in a specimen from Portobello I counted 12 pinnules on anterior edge of the fourth pinna). Anus opens forward of middle of gill membrane on upper side of gill, approximately between the second and third pinnae; anus not raised on a papilla.

Shell (Fig. 8)

Shell large, about half total body length; moderately convex, rectangular and not constricted towards apical (posterior) end; lateral margins nearly parallel; anterior and posterior margins rounded and a little produced beyond level of protoconch (Fig. 8). Protoconch small, white, just over one whorl, not projecting posteriorly but confluent with dorsal surface.

One important distinguishing feature of shell is a whitish flange that projects beyond margin on columellar side (i.e. on left back corner when shell is seen dorsally). This expansion is produced below the spire; it is only weakly developed in juvenile shells but very prominent in large shells.

Sculpture on outside of shell is of numerous, concentric ridges; they often form broad, raised areas with flattened tops. Concentric sculpture is most strongly developed on early and middle regions of teleoconch. Ridges frequently intersect each other; each ridge therefore is of a changing width; ridges run parallel with anterior and right margins, but arch strongly towards posterior margin and left hand edge. Sculpture most clearly visible on smooth area near apex, very similar to that of *B. ornata*; consisting of numerous, fine, wavy ridges and hollows that become obsolete towards the middle part of the shell. I have not yet examined shells with SEM. Shell light golden-brown, with faint, broad, radial streaks of orange-brown; covered externally with a glistening, iridescent periostracum. Shell concave internally, inner surface raised into numerous, irregular, rounded concentric folds separated by flattened areas.

Three shells from specimens taken at Army Bay, Whangaparoa Peninsula, have been deposited in the mollusc collection, Auckland Institute and Museum.

Radula (Fig. 42)

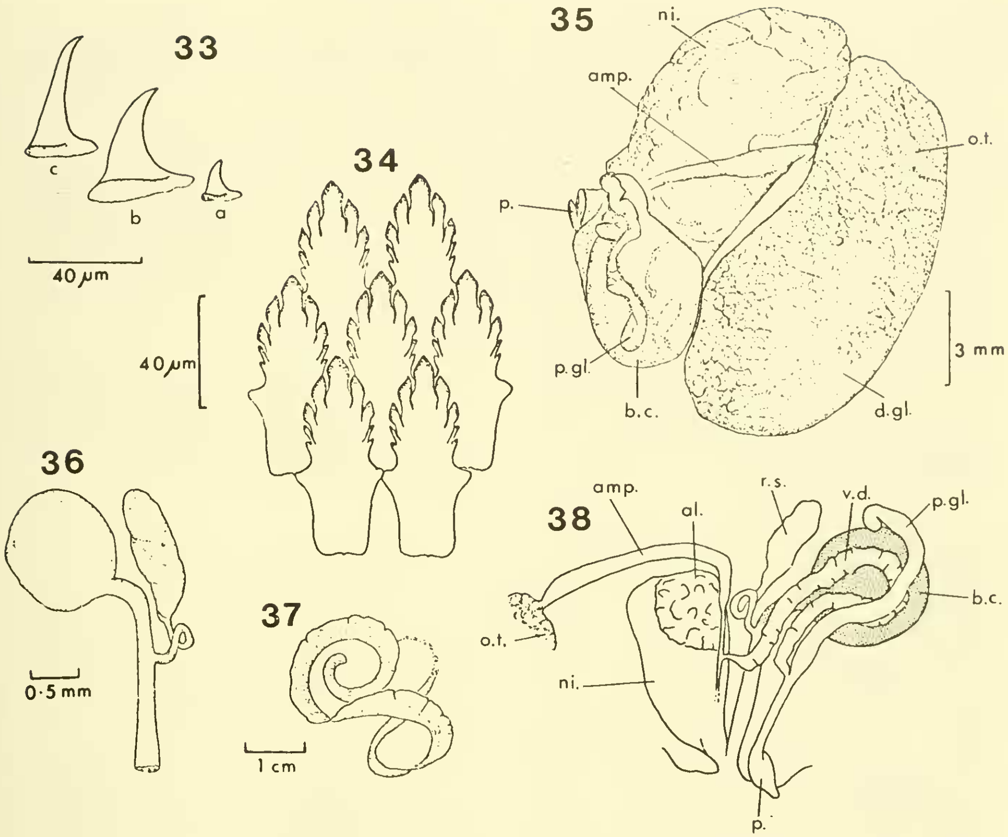
Radula broad, rectangular, expanded towards youngest end; rather small in comparison with radula of similar-sized *Berthella ornata* (largest radula measures—3.0 × 1.8 mm). Rachidian lacking. Lateral teeth numerous, small and without denticulations; inner and middle laterals (Figs. 39–41) similar, broad-based, erect, and ending in a smooth, hooked apex. Lateral teeth increase progressively from the innermost (8 μm high) towards middle (20–30 μm), then outer laterals increase to approx. 35 μm high (Fig. 42). Outer laterals more erect than inner or middle laterals, blades long, straight, apices sharp, only slightly recurved. Extreme outer lateral teeth needle-like, getting progressively smaller.

Numbers of teeth have been remarkably consistent in all radulae examined, with a range of 61 × 65.0.65 to 98 × 76.0.76 (10 radulae). The formula of 56 × 52.0.52 given by Burn (1962) would not appear significantly outside this range.

Jaws

Jaws approximately rectangular, anterior edges rounded. Mandibular elements (Figs. 43, 44) cruciform, sides of blades strongly denticulate. Base of each element narrow (approx. ¼ of total length of 65–70 μm), distance between the lateral processes is 30–35 μm. Strong denticles, which completely occupy sides of blade above lateral processes are most characteristic feature of jaws; denticles coarse, numbers equal or unequal on either side (varying from 3 to 5); denticles point forward, separated by deep grooves; largest denticles immediately adjacent to sharp-pointed apex. Tips of lateral denticles and apices of elements themselves thickened.

Specimens from the North Island and most South Island localities I have examined show little variation in the denticulation of the mandibular elements, and Bergh (1900) illustrated identical elements in a specimen taken near the Chatham Islands. However, two of the jaws from South Island specimens (from Akaroa Harbour and Portobello) have mandibular elements without the characteristic denticulation of the blades and these elements are relatively broader (50–60 μm long, 30–35 μm wide). Sides of blades are irregular but not denticulate, apices are blunt and unthickened; sides taper towards tips. Lateral processes have a relatively larger area of contact with each other than in denticulate elements. Many more jaws require study before it is possible to say whether these variations in



FIGS. 33–38. *Berthella mediatas*. 33. Radular teeth, a = outer lateral, b = middle lateral, c = inner lateral. 34. Group of mandibular elements on inner face of jaw. 35. Reproductive organs *in situ* from the undersurface. 36. Detail of seminal receptacles in a mature animal. 37. Spawn coil. 38. Composite view of structure of reproductive organs. Abbreviations: al. = albumen gland; amp. = ampulla; b.c. = bursa copulatrix; d.gl. = digestive gland; ni. = nidamental glands; o.t. = ovotestis; p. = penis; p.gl. = penial gland; r.s. = receptaculum seminis; v.d. = vas deferens.

mandibular elements are discontinuous as it would appear, or continuous.

Reproductive system (Figs. 35, 36, 38)

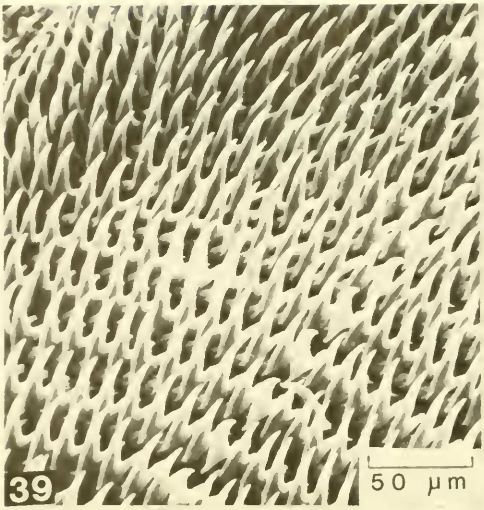
General arrangement similar to that of *Berthella ornata*. Receptaculum seminis of *B. mediatas* an irregular, club-shaped organ arising relatively farther back up vagina, its duct is longer and the receptaculum itself relatively larger. Penial gland elongate, thin-walled, with a recurved tip, relatively longer than that of *B. ornata.*

Egg coil (Fig. 37) loosely spiralled, of about two whorls, flanged, white despite the yellow or brown coloration of *B. mediatas* animals.

Distribution

Berthella mediatas has a continuous distribution throughout New Zealand. Most specimens have been collected from the undersides of intertidal stones and so far there are very few sublittoral records. I suspect the species does not extend deeper than 20 m.

There are several literature records of "*Bouvieria aurantiaca* (Risso)" from southern New Zealand localities: Port Pegasus, Stewart Island (Odhner, 1924); near the Chatham Islands (Bergh, 1900); Masked Island, Auckland Islands (Odhner, 1924); Auckland Islands (Powell, 1955). I have not been able to examine these specimens and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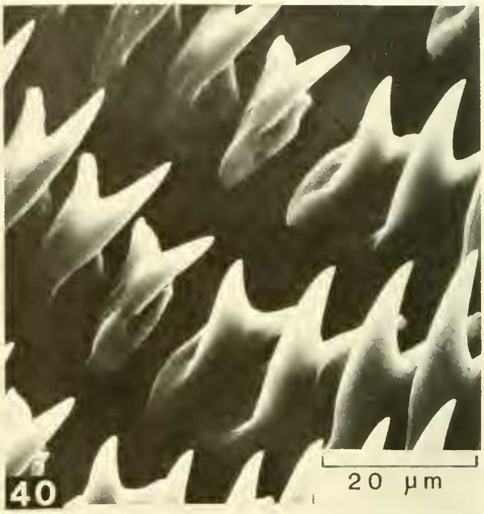
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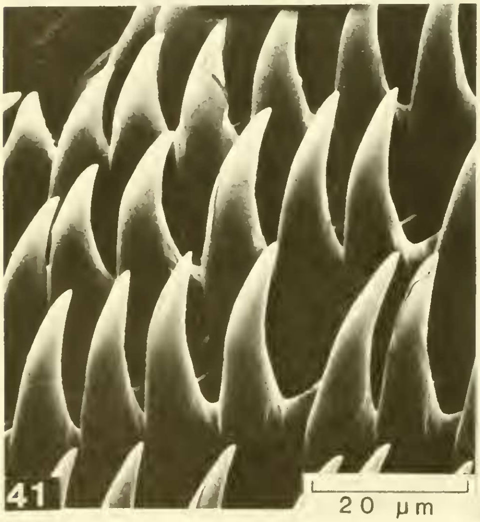
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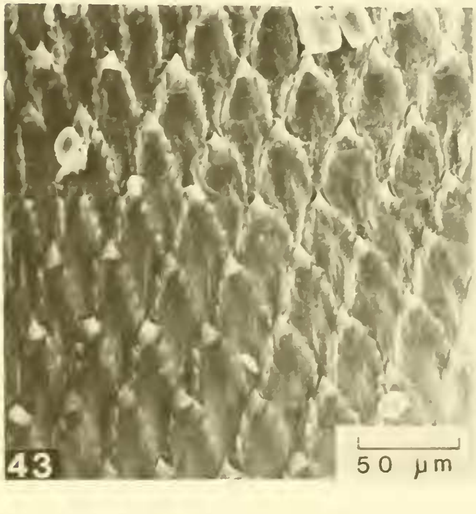
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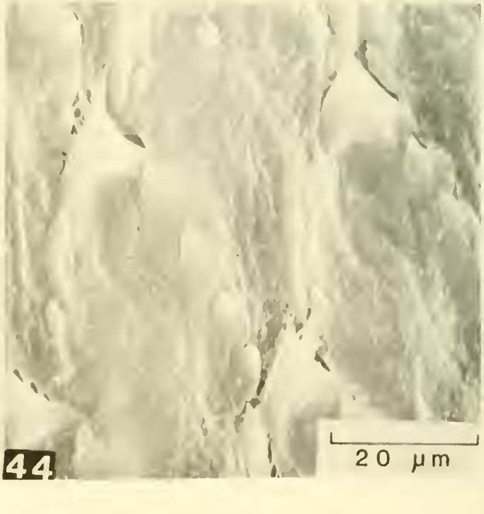
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the only description is Bergh's. However, these are probably all *Berthella mediatas* because the only other yellow or orange pleurobranch from shallow water, *Berthellina citrina,* does not extend farther south than East Cape (North Island). Bergh's (1900) description and figure of his specimen (preserved in sublimated picric acid) are quite sufficient to identify it as *B. mediatas*, although his description is incorrect regarding the site of the anus. Bergh's Chatham Islands locality was confirmed by the specimen taken on Rangitira Island in 1977.

Berthella mediatas also occurs in Australia: Tasmania; South Australia; Victoria; south Western Australia (Burn, 1962, 1966b, 1969, and personal communication). It is the commonest pleurobranch along the Victorian coastline. Thompson (1970) did not record it from eastern Australia, and I found none there during visits in 1975, 1979 and 1980. The New Zealand specimens represent a new locality record. Since *B. mediatas* is already known to have such a wide distribution around the temperate Australian coastline, I would still expect it to be found in southern New South Wales.

Discussion

Confirmation of the presence of *Berthella mediatas* in New Zealand has been achieved by examination of three Australian specimens kindly sent by Mr. R. Burn. Data are as follows: Lorne, Victoria—1 under a stone in a channel on rock platform, R. Burn, 24 Nov. 1974; Warneet, Westernport Bay, Victoria—2 on undersides of stones in sandy area, R. C. Robertson, 15 Sept. 1968. The preserved specimens measured 10.2, 17 and 17 mm long respectively. Not only do they agree with the New Zealand material, but also they have enabled clarification of several points raised by the original description (Burn, 1962). Pedal glands were present on both the larger specimens and the mandibular elements of all specimens had three to five strong denticles on either side of the blade. Both these observations contradict the original description and remove objections regarding the similarity of Australian and New Zealand material. In the Australian specimens the anus opens within the anterior third of the gill basement membrane, generally close to the insertion of the third pinna. This is even further forward than originally described by Burn, he mentioned the anus as being "at the mid-length of the gill membrane."

The name "*Bouvieria aurantiaca* (Risso, 1818)" which has previously been applied indiscriminately in New Zealand to both *Berthellina citrina* (Rüppell & Leuckart) and *Berthella mediatas* Burn should be reserved for a species of *Berthella* from the Mediterranean Sea. The association of the name *Berthella aurantiaca* (Risso) with New Zealand stems from Bergh's (1900) usage. Since then the name has become entrenched and appears in works by Suter (1913), Odhner (1924), Powell (1937, 1939a, 1946, 1955, 1957, 1961, 1976, 1979) and Morton & Miller (1968). Bergh (1900) held the view that the occurrence of *B. aurantiaca* in New Zealand was indicative of one of the more widely-spread forms of opisthobranchs. Probably because of Bergh's reputation and lack of further detailed studies by others, this identification was never challenged. Bergh missed the subtle but significant characters that separate *B. aurantiaca* from *B. mediatas*, and then Suter (1913) compounded the errors by confusing *B. mediatas* and *Berthellina citrina*. Holding no doubt to the same view expressed above, Bergh (1898) reported *Berthella aurantiaca* from Norway, but this record was also subsequently rejected (Odhner 1939).

The two orange pleurobranchs that have been confused in New Zealand can easily be separated since they differ in numerous characters, the most significant of which are summarized in Table 2.

Berthella mediatas shows considerable similarity to some of its congeners in other parts of the world. Fortunately, in New Zealand its separation from *B. ornata* is straightforward. *B. mediatas* appears to have its closest relations in Australia and Europe; separation from these species can be made by reference to Odhner's (1939) and Burn's (1962) thorough studies. The only species that I will distinguish it from is *B. aurantiaca* (Risso). According to descriptions given by Vayssière (1898) and Odhner (1939), *B. aurantiaca* is apricot-orange when alive, al-

◄——

FIGS. 39–44. Radula and jaws of *Berthella mediatas*. 39. Curved inner lateral teeth near midline of radula (midline at top left); note single row of malformed teeth. 40. View of rows of innermost lateral teeth on either side of central row viewed from above; note absence of central row. 41. Detail of curved inner lateral teeth; midline is at upper left; weak serrations on teeth in foreground are artifacts caused by scanning beam. 42. Detail of erect outer lateral teeth. 43. Low-power view of mandibular elements on inner surface of jaw. 44. Detail of same.

TABLE 2. Distinguishing features between *Berthellina citrina* (Rüppell & Leuckart) and *Berthella mediatas* Burn.

Character	*Berthellina citrina*	*Berthella mediatas*
Mantle texture	Smooth, small pores	Many large pores
Shell	Small, triangular, approx. 1/5 body length	Larger, auriculate, approx. 1/2 body length
Anal opening	Hind end of gill membrane	Anterior third of gill membrane
Anterior margin oral veil	Almost straight	Sinuous, deeply cleft mid-anteriorly
Pedal gland	None	Present in adults
Radula	Teeth erect, elongate, denticulate on upper third	Teeth shorter, curved, smooth
Mandibular elements	Blades generally smooth, occasionally with weak denticles	Both sides of blade usually strongly denticulate
Prostate gland	Present	None
Gill	Brownish-cream	Golden-yellow
Spawn coil	White	Golden

most reddish on top. The mantle is translucent and reveals the very large shell beneath; the shell may be up to one-half of the length of the living animal. The anus is at the hind end of the gill membrane. *Berthella aurantiaca* appears to be restricted to the Mediterranean Sea (Bergh, 1892; Vayssière, 1898; Schmeckel, 1968; Barash & Danin, 1971).

Bathyberthella Willan, n. gen.

Definition

Small pleurobranchs; abyssal; body elliptical; mantle smaller than foot, free all round, without an anterior crenulation, smooth; pedal gland present; rhinophores arising together mid-anteriorly; anus at posterior end of gill membrane; shell internal, very large—covering entire viscera, flexible, cuticular, without any calcification; radular teeth very numerous, narrow, erect, smooth, similar across each row, rachidian lacking; mandibular elements oval or elliptical at jaw surface, anterior margin irregularly denticulate; vas deferens dilated into a prostate gland; penis smooth, without accessory structures, penial gland present.

Type-species: *Bathyberthella zelandiae* Willan, n. sp.

The description of this new pleurobranch is included in this present paper so that it is complete for all the known New Zealand Notaspidea. *Bathyberthella zelandiae* is not likely to be taken often because of the depth at which it lives and its fragility.

All known specimens were collected by the New Zealand Oceanographic Institute's research vessel "Tangaroa" whilst it was sampling the benthos of the Bounty Trough on the "Canyon Coral '79" cruise. All the specimens came from two stations close to each other in abyssal depths (>1600 m); they were taken with an epibenthic sled sampling device. A total of 43 specimens was sorted from the stations.

I was fortunate to be present when these pleurobranchs reached the surface in the trawl and were washed from the substratum of light grey ooze. All the animals were moribund when they were sorted from the sample. Those that appeared least damaged were placed in fresh sea water but they did not recover. Despite their moribund condition (all had partially everted buccal masses), the specimens were not dead and it was possible to give an account of the live animal from those that were recovered intact.

Bathyberthella zelandiae Willan, gen. & sp. nov. (Figs. 45–56)

Live animal

Extended body length up to 40 mm. Specimens of all sizes from 5 to 40 mm were represented in this collection. Body oval, globose, very flaccid. Mantle rather delicate, with a definite free border all round, edges thin; surface smooth, no pores apparent; spicules absent; mantle shorter than rhinophores in front, or tail behind. Foot spongy, pedal gland present on sole; pedal gland a large thickened area occupying posterior section of sole but not extending to foot margin, oval, with posterior end wider, oriented at right angles to longitudinal axis of body. Eyes conspicuous, at base of rhinophores, usually large for an abyssal mollusc.

Rhinophores rather short, covered with minute papillae. Oral veil short, anterior margin smooth (i.e. lacking digitations); weakly embayed mid-anteriorly; upper surface papillate (papillae smaller and fewer than on rhinophores).

Gill relatively small in proportion to body length, never extending to level of hind end of mantle; free for about half its length; rachis narrow, smooth; 19–23 pinnae on (upper side of) rachis (mean for 8 specimens—21 pinnae). Anus opens on upper side of gill at hind end of basement membrane; interior longitudinally ridged.

Body creamish, salmon anteriorly; mantle translucent, cream, marked with small, vague, white flecks and speckles, yellow spots occasionally present; digestive gland appearing as a black smudge posteriorly; gill brownish; proboscis salmon.

Shell (Fig. 45)

Shell present beneath mantle in all specimens examined; very large (e.g. 25 × 16 mm in a specimen of 30 mm preserved length); covering entire visceral mass (i.e. it reaches level of front of rhinophores anteriorly). Shell entirely cuticular (without any calcification), very thin and fragile, easily deformed in any direction, disturbance of liquid surrounding shell causes crumpling. Shell concave, broadly oval, a little narrower posteriorly; protoconch not produced beyond posterior margin; shell lacks a posterior flange. Surface flat, concentric growth lines are the only sculpture present, chitin shows localized crumpling caused by compression of overlying mantle during fixation, radial folds present towards margin (particularly anteriorly); a series of regular, undulating ridges present over a small area near apex but ridges are absent over rest of teleoconch. Shell not connected to body muscles or underlying integument. Shell shining, transparent or faintly yellow.

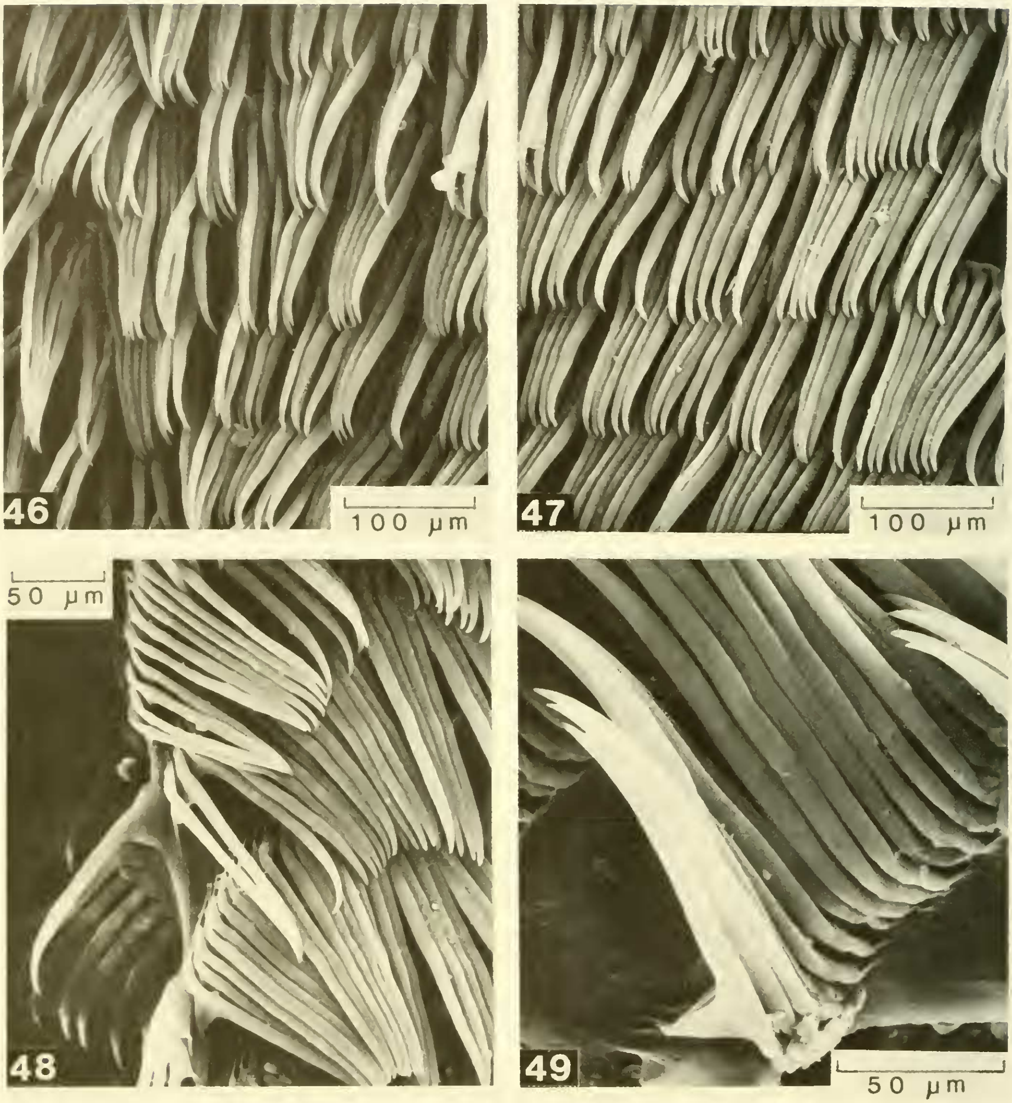
FIG. 45. Shell of *Bathyberthella zelandiae*. Length 23 mm × width 18 mm. Specimen from 1676 m, northern side of Bounty Trough, 26 Oct. 1979.

Two shells from paratypes (NZOI Stn. S152) have been deposited in the wet section of the mollusc collection, National Museum of New Zealand.

Radula (Figs. 46–49)

Buccal mass extremely long, able to be protruded up to half body length. Radula square in appearance, rather short (up to 5 mm in length) and extremely broad through having a very great number of teeth per row. Innermost 40 rows slope very acutely towards midline, remaining rows nearly perpendicular to midline. Central tooth absent. Lateral teeth very numerous, fine, similar in structure across rows, tall and elongate, tapering gradually to a slightly recurved apex; no denticles on blade whatsoever; base triangular, with a thickened posterior area and thin, forward-produced extension, base about five times as broad as middle section of blade.

Inner lateral teeth average 120 μm high (Figs. 46, 47). Middle laterals proportionately higher (155 μm) having base not significantly enlarged. Outermost laterals shorter than middle laterals (95–115 μm); teeth in outer-



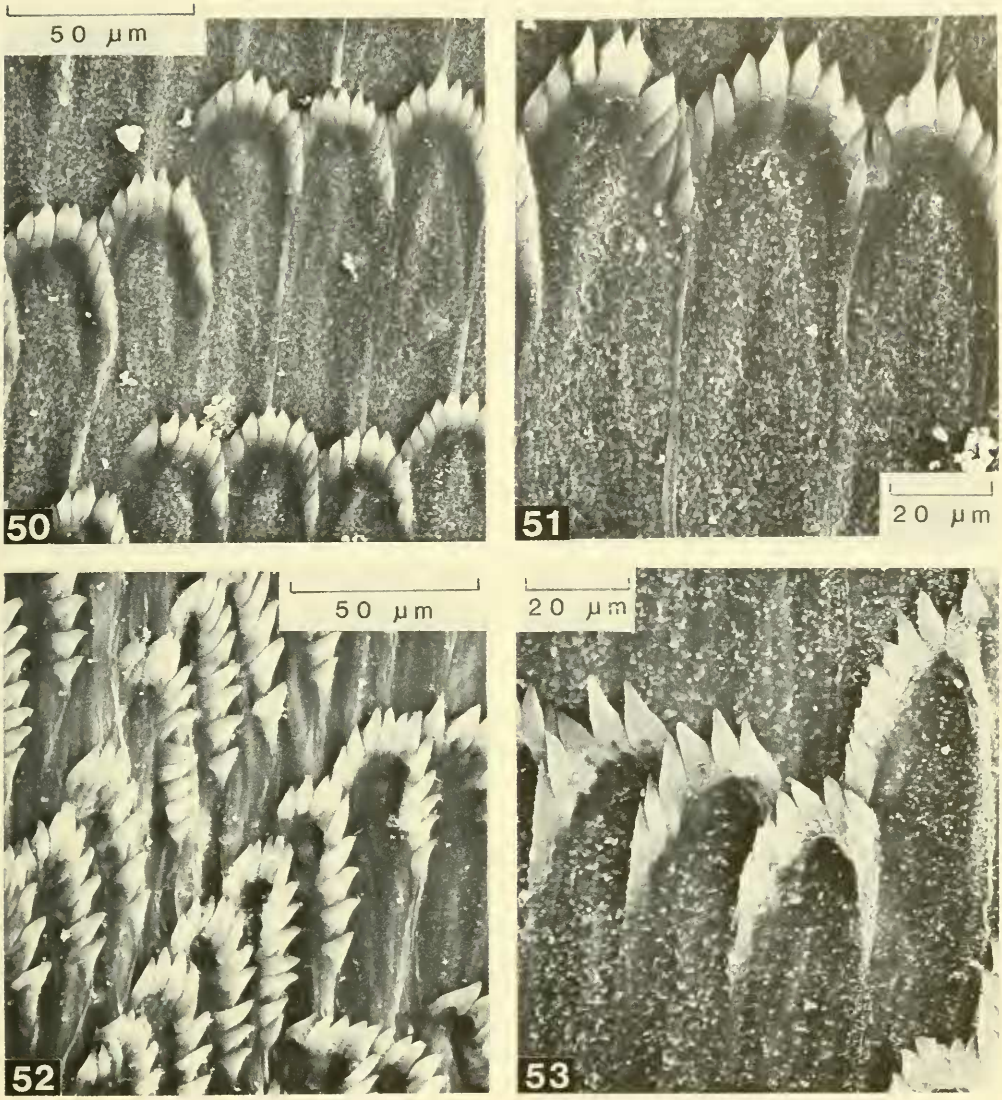
FIGS. 46–49. Radula of *Bathyberthella zelandiae*. 46. Lateral teeth near midline of radula (midline is just to left of centre). 47. Lateral teeth contiguous to those in Fig. 46. 48. Outermost lateral teeth from extreme edge of radula. 49. Detail of same.

most 20 rows become very narrow (only 6 µm wide) and acicular (Figs. 48, 49).

Mean number of rows is 62.1 (standard error = 1.4, radulae from six adults examined). The enormous number of closely-packed laterals prevents an accurate count being made of numbers of teeth per row with a light microscope. Counts of two radulae using a SEM have shown there to be between 210 and 240 lateral teeth. Therefore *Bathyberthella zelandiae* exhibits the following range of radular formulae for adults: 58 × 210.0.210 to 67 × 240.0.240.

Jaws (Figs. 50–53)

Pair of jaws lines buccal mass, about 5 mm in length. Jaws lightly chitinized, blunt anteriorly, tapering to a rounded point posteriorly. Jaws composed of numerous rows of mandibular elements; rows very irregular at surface of jaws, some elements run parallel or slightly



FIGS. 50–53. Jaws of *Bathyberthella zelandiae.* 50. Group of mandibular elements of jaw from a region near centre. 51. Detail of same. 52. Group of mandibular elements towards edge of jaw; note asymmetry of denticles. 53. Detail of same.

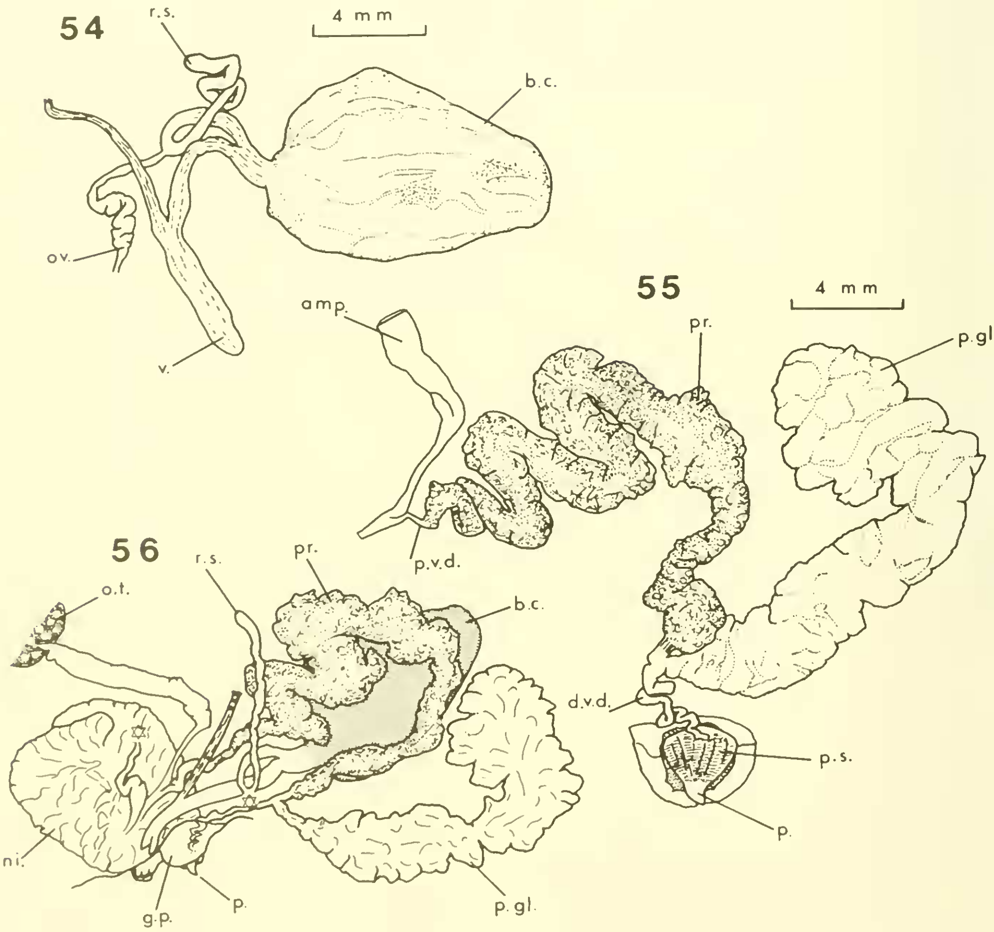
obliquely in groups of 10–12, other elements are considerably displaced from their neighbors to produce highly disorganized patterns; impression of inner surface of jaws is of rows of erratic elements (shagreened appearance). Elements themselves closely-packed (110 μm apart at centre of jaw), elongate or polygonal, bearing a series of thickened, conical denticles along curved, anterior border, the median ones being strongest; elements at centre of jaw possess 4–10 strong denticles arranged symmetrically (Figs. 50, 51); elements towards edges of jaw possess 7–14 weaker denticles that are disposed asymmetrically on leading edge (Figs. 52, 53); denticles towards edges are taller and narrower than those near centre, those towards edges curve away from surface in a claw-like manner (Fig. 53). Denticle numbers are very variable, contiguous elements often have differing numbers; all denticles lack smaller subsidiary denticles.

Reproductive system (Figs. 54–56)

All specimens died with tip of penis protruded from summit of genital papilla; vaginal and oviduct apertures separate. Ampullar region of hermaphrodite duct rather long, smooth-walled, white, flattened, pressed against nidamental glands; it constricts abruptly as it penetrates genital mass between nidamental glands and bursa copulatrix; hermaphrodite duct gives rise to proximal vas deferens before terminating within nidamental complex.

Proximal vas deferens enlarges after a short distance to large prostate gland; prostate gland entwined with penial gland and both are compressed onto bursa copulatrix which they ensheath; prostate moderately thick and spongy; penial gland elongate, tubular, exceedingly thin-walled, fragile, translucent, much-convoluted, dilated distally, wall puckered into pockets; penial gland entirely different in structure to prostate gland. Distal vas deferens long, narrow, thick-walled, it passes into large, conical penial sheath; sheath covered with papillae on outside.

Vagina moderately long, walls ridged internally, possessing a long, narrow muscle slip medially; passing to both bursa copulatrix and receptaculum seminis. Bursa copulatrix dis-



FIGS. 54–56. Reproductive system of *Bathyberthella zelandiae*. 54. Detail of vagina and seminal receptacles. 55. Detail of male section of pallial gonoduct and associated organs. 56. Composite view of structure of reproductive organs, two points marked with asterisks are connected to each other. Abbreviations: amp. = ampulla; b.c. = bursa copulatrix; d.v.d. = distal section of vas deferens; g.p. genital papilla; ni. = nidamental glands; o.t. = ovotestis; o.v. = oviduct; p. = penis; p.gl. = penial gland; pr. = prostate gland; p.s. = penial sheath; p.v.d. = proximal section of vas deferens; r.s. = receptaculum seminis; v. = vagina.

coidal or club-shaped (Fig. 54), walls exceedingly thin, sometimes with weak longitudinal folds. Receptaculum seminis narrow, tubular, much-coiled, approximately equal in diameter to vas deferens; a narrow twisted oviduct originates at base of receptaculum seminis and travels behind retractor muscle to lie at centre of nidamental glands.

Distribution

Bathyberthella zelandiae is only known from the northern slope of the Bounty Trough, southwest of New Zealand. Its bathymetric range is from 1640 to 1676 m.

Type Data

HOLOTYPE: 1676 m, 45°52.3′S; 174° 04.9′E, northern side of Bounty Trough, S.W. of New Zealand (Stn. S152), R.C.W. on G.R.V. "Tangaroa," 26 Oct. 1979 (NZOI, Reg. no. H-342).

PARATYPES: seven specimens (all juveniles), 1640 m, 45°46.0′S, 174°24.5′E, northern side of Bounty Trough, S.W. of New Zealand (Stn. S150) R.C.W. on G.R.V. "Tangaroa," 26 Oct. 1979 (NZOI, Reg. no. P-571); 10 specimens collected with holotype at Stn. S152 (NZOI, Reg. no. P-572); 25 specimens collected with holotype at Stn. S152 (NM).

Discussion

Bathyberthella is a most significant genus within the Pleurobranchidae. This is because *B. zelandiae* possesses an unexpected amalgam of characters some of which are peculiar to it alone and others which relate it to genera of both the accepted pleurobranch subfamilies. The enormous, uncalcified internal shell separates *Bathyberthella* at once from all other genera, but the morphology of the shell is probably related to the abyssal existence of the species. *B. zelandiae* has the external appearance of a member of the subfamily Pleurobranchinae, particularly a species of *Berthella* or *Berthellina*. The reproductive system recalls *Berthellina*, the teeth are smooth as in *Berthella* yet elongate and numerous as in *Berthellina*. These pleurobranchine features strengthen Burn's (1962) contention that the small pleurobranchs (with smooth, non-emarginate mantles and smooth gill rachises) are closer to each other than either is to *Pleurobranchus*. The mandibular elements of *B. zelandiae* show a great likeness to those of *Pleurobranchaea* (subfamily Pleurobranchaeinae).

The bulk of characters favour placing *Bathyberthella* in the Pleurobranchinae. Within that subfamily is another equally anomalous, yet important, monotypic genus—*Pleurehdera*. *Pleurehdera haraldi* is small; it has a smooth mantle and gill rachis; it possesses a pedal gland, prostate gland and penial gland; its teeth are elongate, most possess a single denticle near the apex but the outermost laterals are smooth for about one quarter of the row; the mandibular elements are variable (Marcus & Marcus, 1970). Some of the variation shown by the mandibular elements of *Pleurehdera haraldi* resemble those of *Bathyberthella zelandiae.* Even allowing for the abyssal habitat of *B. zelandiae,* the differences between shells, radulae and reproductive systems of *Pleurehdera* and *Bathyberthella* indicate they are not congeneric.

I interpret *Pleurehdera* and *Bathyberthella* as terminations of narrow lines produced during the radiation that followed the acquisition of the pleurobranch grade of organization by opisthobranchs. Both these genera stem from near the *Berthella*/*Berthellina* dichotomy. The genera *Euselenops* and *Pleurobranchella* illustrate analogous cases; they probably represent terminations of narrow side lines that originated on the pleurobranchaeine side of this radiation. I cannot interpret any of these monotypic (or very small) genera as ancestral to any large present day genus. This is because all the small genera possess a mosaic of characters many of which are quite unlike those of their presumed derivatives. One point that emerges is that the oval type of mandibular elements with denticulate anterior borders (as in the Pleurobranchaeinae) preceded the cruciform type of elements (as in the Pleurobranchinae).

It is unlikely that *Bathyberthella zelandiae* could be confused with either of the two small, yellow or orange pleurobranchs from New Zealand that look superficially similar (*Berthella citrina, Berthella mediatas*) since both the latter occur in shallow water on the continental shelf. Listing the many points of difference between these three species would involve repetition, in a comparative context, of diagnostic characters for each genus and reconstruction of a table similar to Table 2 (p. 248) to incorporate *B. zelandiae.* Comparisons of the significant characters between these three species will be presented in the key and repetition of the more subtle points of distinction is unnecessary in view of the abyssal habitat of *B. zelandiae* and the scarcity with which it is likely to be encountered.

Pleurobranchaea Meckel in Leue, 1813

Pleurobranchaea Meckel in Leue, 1813: 11. Type-species by subsequent monotypy (Blainville, 1825: 376): *Pleurobranchidium meckelii* Blainville, 1825.

Pleurobranchidium Blainville, 1825: 372, 376. Type-species by monotypy: *Pleurobranchidium meckelii* Blainville, 1825.

Koonsia Verrill, 1882: 545. Type-species by monotypy: *Koonsia obesa* Verrill, 1882.

Pleurobranchillus Bergh, 1892: 27. Type-species by subsequent designation (Willan, 1977: 153): *Pleurobranchillus morosus* Bergh, 1892.

Meckel (in Leue, 1813) established *Pleurobranchaea* without including nominal species. Blainville (1825) was the first author to describe the species *meckelii* in the genus *Pleurobranchaea,* and it is this species *ipso facto* which becomes the type of *Pleurobranchaea* by subsequent monotypy. According to the International Code of Zoological Nomenclature, the spelling must revert to *meckelii* (from *meckeli*) since this is the correct original spelling (Art. 32(1), I.C.Z.N. 1961). I have considered the synonymy of *Koonsia* and *Pleurobranchillus* elsewhere (Willan, 1977). Bergh (1897: 3, note 2; 1898: 64) himself subsequently recognized *Pleurobranchillus* as a synonym of *Pleurobranchaea* (see Vayssière, 1901: 74; and Marcus & Marcus, 1957: 25).

Definition

Moderate-sized to large pleurobranchs with oval or oblong bodies that are blunt anteriorly; mantle reduced, smaller than foot, merging with oral veil anteriorly and tail posteriorly, covered with low tubercles; rhinophores far apart, inserted on either side of head at base of oral veil; oral veil with digitate processes along anterior margin; pedal gland present on posterior part of foot sole in sexually mature specimens; some species possess a caudal spur on dorsal side of tail; anus towards rear of gill basement membrane; shell absent; buccal mass relatively large; radula with central row, laterals curved, smooth-sided, most with an accessory denticle—either strongly or weakly developed; mandibular elements polygonal or rounded at jaw surface, denticulate along anterior edge; penis without accessory leaves; prostate gland present.

Remarks

As with all the Notaspidea, species of *Pleurobranchaea* often show considerable intraspecific variability and this has frequently resulted in the creation of spurious species. This cause for uncertainty has been compounded by inadequate description of new species based on poorly fixed material. Nevertheless there are subtle and consistent differences separating the valid species.

Marcus & Marcus (1957) and Marcus (1957) listed the 18 described species of *Pleurobranchaea*; they later claimed that *P. algoensis* Thiele and *P. japonica* Thiele were unrecognizable (Marcus & Marcus, 1966). Four species have been added since the Marcus' first lists: *P. hamva* Marcus (1957); *P. gemini* Macnae (1962), *P. californica* MacFarland (1966); *P. gela* Marcus & Marcus (1966). More material, however, has forced *P. hamva* to be incorporated into the synonymy of *P. hedgpethi* Abbott (Marcus & Marcus, 1967b).

Much more work needs to be done on this genus; for example, to determine the status of such species as *Pleurobranchaea capensis* Vayssière, 1898, *P. gemini* Macnae, 1962, *P. brocki* Bergh, 1897 and *P. agassizi* Bergh, 1897. Some new species are known and await description.

Because of their large size, high level of activity and variety of relatively complex behaviours, species of *Pleurobranchaea* are now frequently used in physiological research, e.g. Davis and Mpitsos (1971), Davis *et al.* (1977), and this is further reason to reexamine the taxonomic status of the various entities.

Pleurobranchaea maculata (Quoy & Gaimard, 1832) (Figs. 57–70)

1832. *Pleurobranchidium maculatum* Quoy & Gaimard: 301, pl. 22, figs. 11–14.

1878. *Pleurobranchaea novaezealandiae* Cheeseman: 276, pl. 15, fig. 3.—1879, Cheeseman: 378, pl. 16, fig. 3—1880, Hutton: 124.—1896, Pilsbry: 227, pl. 53, fig. 87.—1897, Bergh: 150–152, No. 31 and 154–155 No. 33.—1913, Suter: 553.—1915, Suter: pl. 36, fig. 2.—1933, Allan: 446.—1949, Baba: 133, pl. 10, figs. 31, 32, 34.—1957, Burn: 12, 15.—1957, Marcus & Marcus: 26.—1965, Guang-Yu & Si: 266, 275; 1966, Marcus & Marcus: 177.—1969, Baba: 191.—1976, Powell: 112.—1979, Powell: 282, pl. 51, fig. 2.

1896. *Pleurobranchaea maculata* (Quoy & Gaimard); Pilsbry: 227, pl. 53, figs. 88, 89.—1897, Bergh: 153–154, No. 32.—1901, Vayssière: 49–56, pl. 5, figs. 238–247.—1913, Suter: 552.— 1915, Suter: pl. 23, fig. 17.—1924, Odhner: 52.—1937, Powell: 85, No. 1236.—1954, Pruvot-Fol: 33.—1957, Marcus & Marcus: 26.—1958, Burn: 6.—1966a, Burn: 271.—1966b, Burn: 106.—1969, Burn: 80.—1970, Thompson: 192–195, fig. 10.—1976, Powell: 112.—1977, Gordon & Ballantine: 40, 112.—1979, Powell: 283.

1898. *Pleurobranchaea novaezelandiae* [sic] Vayssière: pl. 15, fig. 28.—1901, Vayssière: 69–72.—1900, Bergh: 208, pl. 20, figs. 56, 57, pl. 21, fig. 69.—1920, Mestayer: 170–171.—1924, Odhner: 52.—1937, Powell: 85, No. 1234.—1961, Powell: 107.—1964, Williams: 20.—1968, Morton & Miller: 167, 576, pl. 11, fig. 8.—1969, Batham: 78.—1970, Thompson 196.—1972, Morton: 346.—1973, Miller & Batt: 19, fig. 78 (image reversed during printing).—1977, Willan: 154.—1977a, Ottaway: 217–218.—1977b, Ottaway: 125–130, fig. 1 (error pro *P. novaezealandiae* Cheeseman, 1878).

1900. *Pleurobranchaea novaezelandiae* var. *granulosa* Bergh: 209.—1913, Suter: 554 (as ssp. *granulosa*).—1937b, Powell: 85, No. 1235 (as ssp. *granulosa*).—1961, Powell: 107 (as ssp. *granulosa*).

1933. *Pleurobranchaea dorsalis* Allan: 445, pl. 56, figs. 4, 5.—1957, Marcus & Marcus: 26.

1950. *Pleurobranchaea maculata dorsalis* Allan: 208, fig. 1.

1976. *Pleurobranchaea granulosa* Bergh; Powell: 112.—1979, Powell: 282.

The original description of *Pleurobranchidium maculatum* by Quoy & Gaimard (1832) was brief and dealt only with external features. The description was greatly expanded by Vayssière (1901) after a thorough re-examination of the type material. Vayssière (1901) detected a mistake made by Quoy & Gaimard (1832) with respect to *Pleurobranchaea maculata*. Vayssière had examined the (five) specimens collected by "l'Astrolabe" and he expressed astonishment that "Nouvelle-Zélande" was given as the locality on the labels on three of the five original specimens. Quoy & Gaimard (1832) stated that all had originated from Port Western to Jarvis Bay, Australia. Vayssière suspected that Quoy & Gaimard had erroneously labelled those three specimens; he did note, however, that New Zealand was included as part of the original locality citation for *Pleurobranchaea maculata*.

My investigations have shown that there is only a single species of *Pleurobranchaea* in New Zealand, for which the name *Pleurobranchaea maculata* (Quoy & Gaimard) has priority. No consistent differences can be found to warrant the continued separation of New Zealand specimens under the names of *P. novaezealandiae* Cheeseman or *P. novaezelandiae granulosa* Bergh (see below). Several other authors have already anticipated the synonymy of *P. novaezealandiae* with *P. maculata*. In her discussion, Pruvot-Fol (1954: 33) concluded by reiterating Vayssière's remark that the two might well be variants of a single species. Burn (1958) synonymized *P. novaezealandiae* and the Australian *P. dorsalis* Allan with *P. maculata*. Thompson (1970) suggested that all the Australian records of *Pleurobranchaea* are based on *P. maculata* (Quoy & Gaimard).

Live animal (Fig. 57)

Body large, elongate, oval, covered dorsally by a relatively small mantle beneath which foot projects all round. Mantle confluent anteriorly with oral veil, posteriorly it is continuous, over a relatively narrow area, with tail; sides of mantle free, left border held close to body, right slightly larger, held away from body to accommodate gill underneath. Mantle smooth, soft, upper surface (and that of oral veil) entirely covered with minute puckers and folds. Ground colour varies from pale grey to almost ash-black, broken by irregular, pale, grey-white areas to give a dappled-reticulate appearance. Raised areas sprinkled with numerous, minute, and almost microscopic, white dots; hollows between these raised areas darker. Some individuals uniformly dark, others have paler areas and a patchy appearance. Auckland east coast populations appear to show approximately equal proportions of dark and dappled morphs. Undersurface of free mantle borders smooth, grey,

FIG. 57. *Pleurobranchaea maculata* (Quoy & Gaimard). Length = 132 mm. Specimen from 7–11 m, off middle head of German Bay Hill, Akaroa Hbr., Banks Pen., May 1962. Photograph: M. C. Miller.

regularly speckled with white dots. Mantle discharges a clear fluid of pH = 1.

Oral veil trapezoidal, lower surface smoother than upper surface; it bears some raised pustulose areas forming weak reticulations; anterior border of veil broad, straight, wider than widest part of body when animal is crawling. Anterior corners project laterally beyond front edge. Lateral areas marked dorsally by a white line. On undersurface, a groove extends length of lateral areas; here each area appears as a brownish streak. All along anterior edge of oral veil are many, small, branched processes; therefore oral veil of *Pleurobranchaea* species is more elaborate than that of *Berthellina* or *Berthella* species. The increased structural complexity is accompanied by increased activity; when animal is crawling actively, anterior border constantly ripples as it explores substratum in different areas.

Rhinophores arise laterally where the mantle passes into oral veil; mottled grey and white, tipped with white.

Gill large, conspicuous, generally its hind end extends beyond overlying right mantle flap; basement membrane attached to gill for approximately half its length.

Gill rachis bears 20–28 alternating pinnae (mean number for 9 specimens 23.0); pinnae relatively longer than in species of *Berthellina* or *Berthella*; pinnae bear large numbers of closely-packed pinnules (25–30 on anterior pinnae); rachis itself broad, flattened, with small, irregular knobs and lumps; however, rachises of pinnae round, smooth. In living specimens, gill is light ash-grey, with rachis and rachises of pinnae overlain with tiny black specks. This superficial speckled layer rubs off with ease in newly dead specimens, revealing a subepidermal layer of larger, opaque, white spots which does not rub off. Anus opens a short distance in front of hind end of the gill basement membrane. Prebranchial aperture conspicuous, on a papilla before front of gill rachis, interior ridged.

Foot broadly rounded anteriorly, more pointed behind; upper surface similar in colour and pattern to mantle; foot borders thin and with white puckers that are more regular than on mantle. Anterior dorsal surface with a clearly demarcated, broad, greyish mucous groove; this area being wider than area of the foot overhung by oral veil. Mucous groove has a deep, mid-anterior cleft perpendicular to its axis. Sole of foot very large, smooth, pale ash-grey, lightly speckled with white, margin white. Pedal gland present posteriorly in sexually mature individuals, lying beneath foot epithelium, length about 1/6 total length of the foot; pedal gland somewhat asymmetric and triangular with base (closest to tail) shorter than sides; base does not reach extremity of tail. The white buccal mass and dark digestive gland are visible through transparent tissue of foot sole. Caudal spur never present on dorsal surface of tail.

Pleurobranchaea maculata is able to float upside-down on the meniscus in a still container of water, then lateral and posterior foot margins show slight indentations.

Animals are normally encountered at rest on undersides of stones, foot and body contracted and humped up; mantle rounded, gill extending beyond right border, pinnae twitching occasionally quite independently of each other; oral veil contracted against anterior mantle edge; rhinophores held laterally in groove formed by oral veil and mantle.

Radula (Figs. 58–63)

Radula large (8.4 mm long for a specimen 37 mm in extended length), relatively broad, deeply grooved in midline, with many rows of

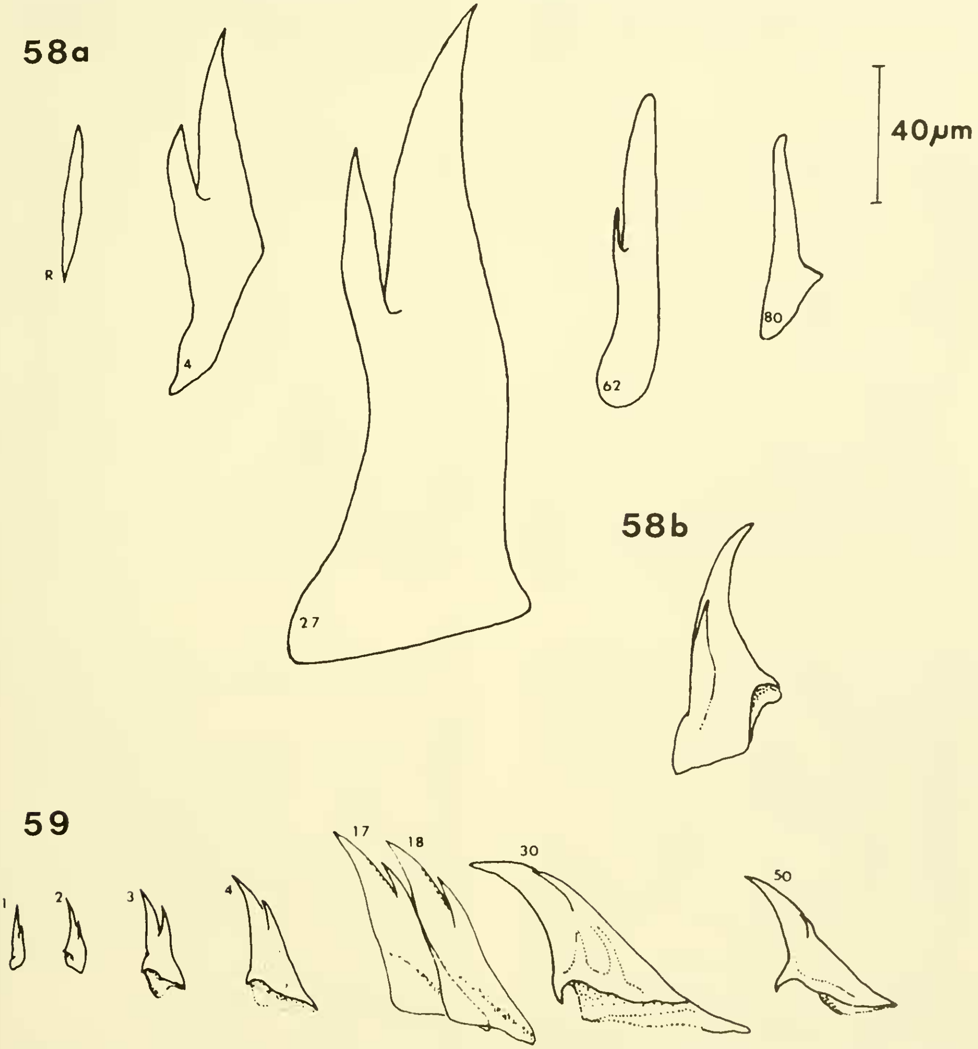


FIG. 58, 59. Radula of *Pleurobranchaea maculata*. 58a. Representative teeth from a half row; 58b. Middle lateral tooth showing detail of basal attachment region; 59. Teeth from a half row (after Vayssière, 1901, pl. 5, figs. 238–240, 242).

lateral teeth symmetrically on either side of central row. Radula of adult *P. maculata* has 40–50 rows. Rachidian inconspicuous, short (approx. 30 μm high), narrow, with a rounded base and pointed apex; apparently constant in length in all rows. Careful preparation is necessary to keep rachidian on radula; despite its presence in all rows, it fell away in most cases during preparation of radula.

There are 70–80 lateral teeth within each half-row; laterals undergo characteristic changes in size and structure across rows. Outermost lateral teeth (Fig. 63) small, peg-like, narrow, rounded apically with apices slightly recurved; extreme outermost teeth (number 80 counting from midline) smallest, approx. 48 μm high. By 65th lateral, a small spike is present on inner side near base of tooth, cusp of tooth itself sharper; at this point teeth are up to 60 μm high. Teeth continue to get larger, and lateral spike enlarges to a strong accessory denticle increasing in size, so that by 41st tooth (approx. mid-way across row) denticle is 64 μm high, the tooth itself being 298 μm high. In this middle region teeth have large, broad bases, sides parallel to point where denticle arises, beyond there sides curve inwards to sharp apex; lateral denticle straight-sided and erect (Figs. 61, 62). To the inside of this region, teeth again slowly decrease progressively although lateral denticle remains nearly same height. Close to rachidian there is a rapid decrease, teeth and denticles decreasing proportionately, second lateral approx. 60 μm high and still bears a small accessory denticle.

A radular formula typical of an adult is 43 × 74.1.74. The range of radular formulae for adult New Zealand specimens examined is 40–50 × 70–80.1.70–80. Radular formula increases as *P. maculata* grows; a juvenile (crawling length 5 mm) from Cape Three Points, Akaroa Harbour, had a formula of 25 × 39.0.39; tooth height also increases proportionately with growth.

System for attachment of teeth to basement membrane like that of *Pleurobranchaea californica* (MacFarland, 1966: 97), although the basal facets are knobbed rather than hook-like in *P. maculata* (Figs. 61, 63). System for support of teeth along rows also present; outer laterals (Fig. 63) have a socket towards base where right-angled elbow of base of tooth in front fits, same interlocking arrangement present between middle lateral teeth (Fig. 61).

Tooth structure is a very constant and characteristic feature of *Pleurobranchaea maculata*, particularly the strong, accessory lateral denticle on middle lateral teeth. *P. californica* has very small, weak denticles (MacFarland, 1966). I have redrawn Vayssière's (1901, pl. 5) illustration of isolated radular teeth from specimens of the type lot of *P. maculata* (Fig. 59); they show a strong resemblance to New Zealand material.

Jaws (Figs. 64, 65)

A pair of elongate, chitinous jaws lines inside of buccal bulb; rectangular; hind portion expanded and rounded, anterior margin deeply sinuate, with a forward-projecting spike towards centre. Many tightly-fitting, polygonal elements, in the form of closely-packed columns make up jaws; surfaces of elements flattened, resembling interlocking paving stones; elements arranged in alternating rows (about 60 per row), mostly hexagonal though some are pentagonal or round. From the surface, base and sides of elements appear smooth, sides are parallel, slightly longer than the base; there are no lateral projections. On broadly convex anterior face are 5–12 small, pointed denticles; denticles not positioned symmetrically about anterior edge. Central area on inner face is irregularly pustulose (Fig. 65). Average dimensions of elements are: length 40 μm; width 60 μm.

MacFarland (1966) studied the development of mandibular elements in *Pleurobranchaea californica*.

Reproductive system (Figs. 66–69)

To expose the reproductive system in dissection, the network of anastomosing tubules of dorsal accessory gland must first be removed; these fine tubules surround all organs of reproductive system and gut. Because the

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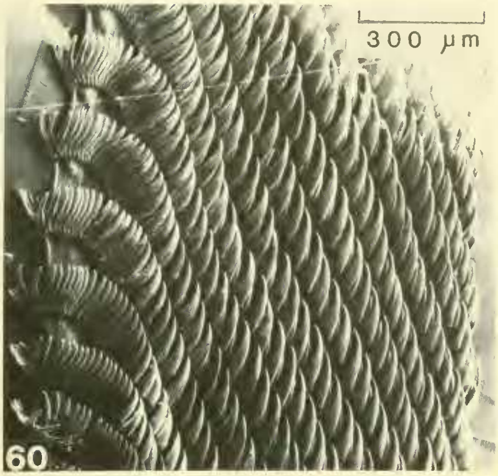
FIGS. 60–65. Radula and jaws of *Pleurobranchaea maculata*. 60. Teeth on one half of the radula; outermost laterals are on the extreme left. 61. Detail of large, middle lateral tooth; note accessory denticle on each tooth. 62. Detail of same; longitudinal striations are probably dried mucus. 63. Detail of small, peg-like outermost lateral teeth. 64. Mandibular elements on inner face of jaw. 65. Detail of the same.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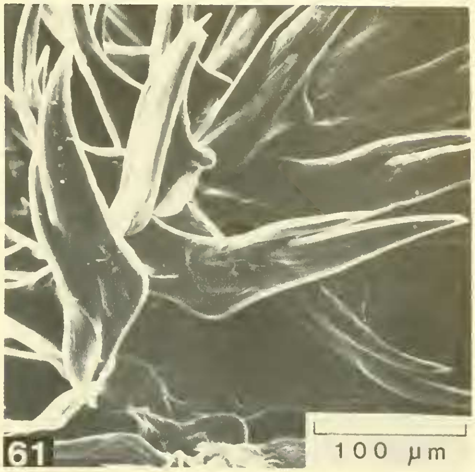
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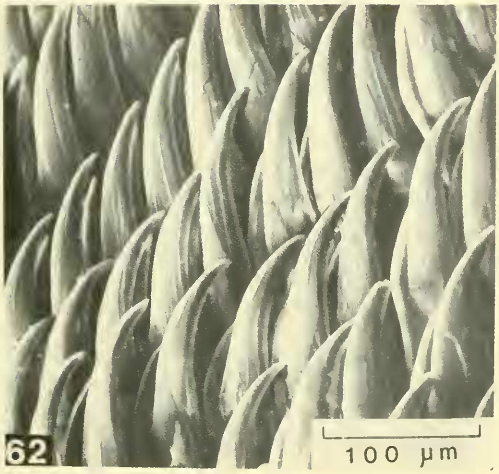
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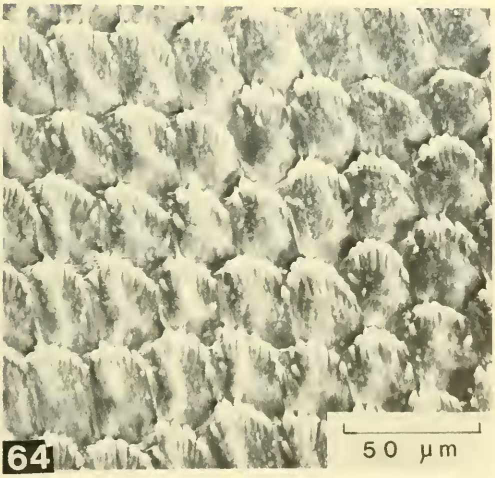
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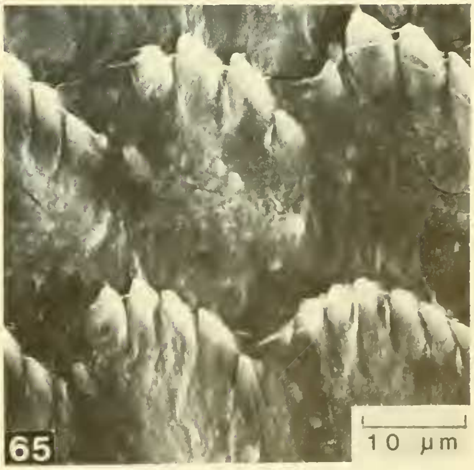
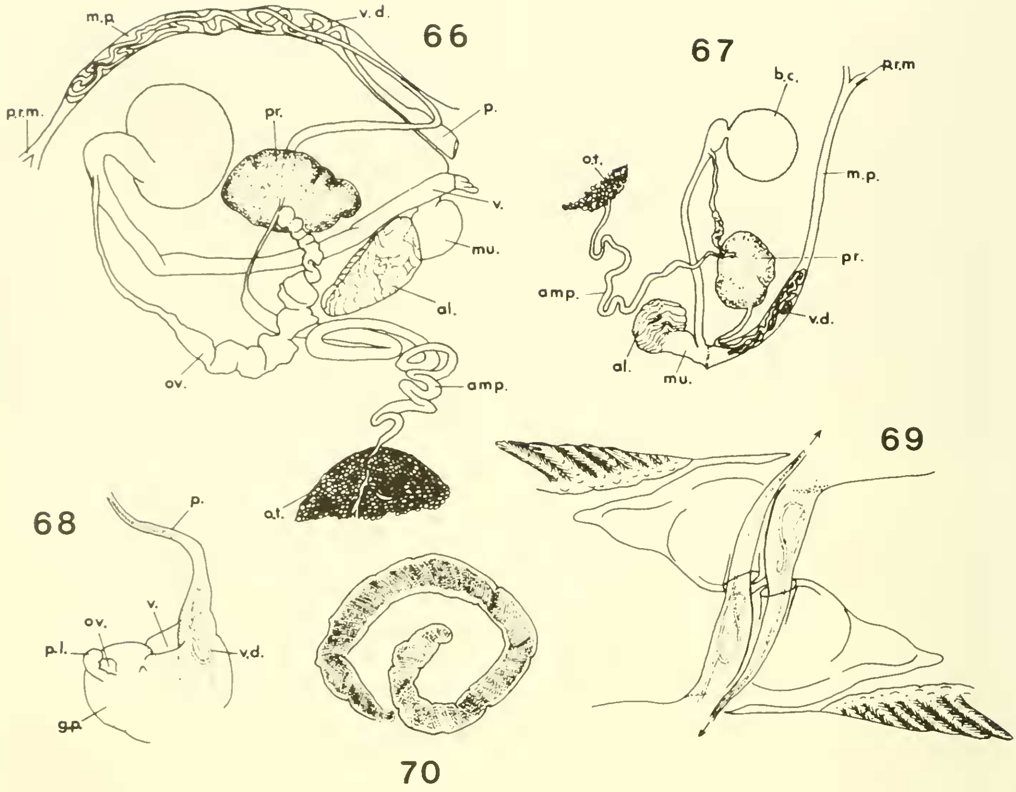

65



FIGS. 66–70. Reproductive system of *Pleurobranchaea maculata*. 66. Composite view of structure of reproductive organs. 67. Reproductive system of a paratype (after Vayssière, 1901, pl. 5, fig. 247). 68. Detail of fully everted genital organs. 69. Orientation of genital organs during reciprocal copulation, arrows indicate direction of sperm injection into bursa copulatrix of partner. 70. Spawn mass. Abbreviations: al. = albumen gland; amp. = ampulla; b.c. = bursa copulatrix; g.p. = genital papilla; m.p. = muscular pocket for vas deferens; mu. = mucous gland; o.t. = ovotestis; ov. = oviduct; p. = penis; p.l. = posterior lobe of everted genital papilla; pr. = prostate gland; p.r.m. = penial retractor muscle; v. = vagina; v.d. = vas deferens.

structure of the reproductive organs differs in many ways from that of species of the Pleurobranchinae, it is described here in full.

Ovotestis dorsal, applied to, but not interlobed with, digestive gland; creamish-white, compact, appearing granular because of elongate acini stacked side by side. Inside ovotestis, fine white collecting ducts can be traced amongst acini; these smaller ducts join larger and larger ducts, finally to a still slender, sinuous, white hermaphrodite duct with ovotestis on its anterior ventral surface. Immediately upon leaving ovotestis, hermaphrodite duct greatly increases in diameter and wall thickness to form ampulla. Ampulla lies next to foot musculature, much coiled and convoluted; it gradually enlarges as it passes towards ventral midline. Near midline, ampulla turns forward (below nidamental complex), and abruptly narrows to about ¼ of its previous diameter, now becoming quite straight; it branches into two, and, after becoming a very short, but slightly wider proximal vas deferens, enters prostate gland.

Oviduct is the other of these branches; at its point of origin from hermaphrodite duct (beside the prostate gland), oviduct is large, its walls deeply constricted, of a greater diameter than hermaphrodite duct, thickest approx. ⅓ of the distance along its length, after that diameter is halved. Oviduct next travels as a straight, whitish tube beneath bursa copulatrix to join much larger vagina before the latter passes into bursa copulatrix.

Bursa copulatrix varies in position and shape; it lies, *in situ*, in midline, either dorsally, above the buccal mass and visceral ganglia, or ventrally, below and next to them.

Bursa generally discoidal or club-like, flat beneath and convex above. Vagina completes a half loop on dorsal side of bursa before passing into it; end of the vagina connected to bursa is neither swollen nor constricted. Recepaculum seminis absent.

Vagina slowly increases in diameter as it passes, in a semicircle, beneath all the reproductive organs, to exterior. Vagina is tube of greatest width in reproductive system; it is whitish, its walls are tough and unconstricted. Nidamental gland complex situated besides vagina—mucous gland orange, relatively thin-walled; albumen gland larger, more solid, cone-shaped, walls much-convoluted.

Vas deferens is a continuation of hermaphrodite duct from the point at which oviduct departs; proximal vas deferens is visible for only a very short distance before entering prostate gland. Prostate gland irregular in outline and size, spongy, consisting of many tightly-packed vesicles. Distal vas deferens leaves prostate gland, its walls thickened and shining. Just beside the penis, distal vas deferens curves backwards into an elongate pocket of clear and tough tissue; pocket passes backwards above prostate gland, female glands and digestive gland, then travels to foot where retractor muscles attach it to floor of body cavity; this pocket is the most conspicuous part of entire genital system. Distal vas deferens lies within pocket, it often loops over itself, it retains its same diameter throughout entire course after leaving prostate gland. Towards the end of its course back inside pocket vas deferens expands gradually into penis. Penis is long, narrow, smooth-walled, quite smooth, capable of eversion to a great distance.

The organization of the reproductive system in New Zealand *Pleurobranchaea* material presents one of the strongest reasons for believing it to be conspecific with *P. maculata* (Quoy & Gaimard). The system detailed above (Fig. 66) is almost identical with that described by Vayssière (1901) for specimens from the type lot (Fig. 67).

The reproductive system in this genus is highly diagnostic for each species. In *Pleurobranchaea meckelii* the pocket for the vas deferens is shaped like a large, inverted cone and the retractor muscle is inserted on the body wall; in this species too, the oviduct has a short proximal tube followed by two ovoid swellings; the shape of the bursa copulatrix is also different. The enigmatic caudal spur is present on the post-dorsal surface of the foot.

Behaviour at copulation and oviposition

Not only is the organization of genital organs important in species recognition, but also reproductive behaviour is highly species-specific. *Pleurobranchaea* species tend to be solitary, so mating encounters occur seldom and have been reported very infrequently in the literature. Davis & Mpitsos (1971) give details of copulatory behaviour in *P. californica*. The following account describes the mating behaviour of *P. maculata* in detail.

When two mature specimens of *Pleurobranchaea maculata* encounter each other, one of two behaviour patterns results. Upon contact one animal rapidly everts its oral tube and makes feeding thrusts towards the other; often removing a piece of flesh. Most attacks of this kind appear to be directed at the tail region. This type of behaviour most often results from initial contact of the oral veil of one specimen, with some other part of the other specimen. The attacked animal may let go of the substratum and swim with head-to-tail flexions to avoid further attacks.

The second response often occurs when two specimens meet head first. After the oral veils contact each other, forward motion slows, both partners raise their right mantle edges, and partially evert their genital organs. This is a very characteristic sexual posture. It is often followed by mutual circling during which the genital organs are fully everted, and the long, whip-like penis is rapidly everted and thrust in the general region of the reproductive apertures and gill.

In the laboratory, following an encounter of this type, one partner frequently fails to reciprocate and crawls away. But if both animals are receptive at that time, circling and penial thrusting continue. The penis is retracted and fully everted repeatedly but the posterior swelling that exposes the vagina remains everted and distended. Behind the vagina this swelling becomes lobed and narrows to a tail-like extremity (Fig. 68).

When the penis of one partner is correctly thrust towards the vaginal entrance, the penis enters and passes a considerable distance into the vagina (the tip probably reaches the base of the bursa copulatrix). Copulation is most often reciprocal by this stage, and Fig. 69 shows the position of everted genitalia and penial insertion in such a reciprocal copulation. Copulation lasts less than two minutes.

Oviposition lasts one or two hours. The egg mass (Fig. 70) is usually in the form of a loose and irregular coil of approximately 1½ whorls, but this pattern is not circumscribed as in the Pleurobranchinae; some egg masses are irregulary looped, others open. Larger individuals lay larger coils. The egg mass is circular in cross section and is composed of a clear, gelatinous outer area inside which the long string of white eggs is tightly coiled; coiling is generally oblique to the outer wall. The egg mass is attached to the substratum by a narrow, opaque-white strip which frequently persists after the mass has disintegrated. Mestayer (1920) and Graham (1941) have recorded observations and given photographs of aquarium spawning in *Pleurobranchaea maculata*.

Larvae hatch after approximately 10 days; they are planktonic veligers with a small cuplike shell and operculum. Veliger shells are 180–200 μm long and approx. 120 μm wide. In aquaria, settlement was observed after six days but could be delayed for at least one week. The larvae can feed in the plankton; larvae, experimentally fed with a suspension of *Dunaliella primolecta*, ingested these cells. Further aspects of the planktonic life and settlement of veligers were not studied.

Distribution

Pleurobranchaea maculata occurs throughout New Zealand. It lives both intertidally and subtidally (to at least 300 m) and appears to be equally abundant through that entire bathymetric range. Specimens are most frequently encountered nesting in depressions on the undersurfaces of stones; when uncovered they immediately start crawling to safety.

Pleurobranchaea maculata is more tolerant than other pleurobranchs of waters carrying suspended silt, and thus appears in harbours and estuaries where the others are absent. This is probably also correlated with food; *P. maculata* is an opportunistic carnivore and can take advantage of a wide range of prey species, whereas other pleurobranchs feed on species of sponge or ascidians which are themselves confined to clear water situations.

Pleurobranchaea maculata also occurs in southern Queensland (Burn, 1966a), New South Wales (Allan, 1950; Thompson, 1970), Victoria, Australia (Burn, 1957, 1966, 1969), China (Tchang-Si, 1934; Guang-Yu & Si, 1965), Sri Lanka (White, 1948) and Japan (Baba, 1937, 1949, 1969; Baba & Hamatani, 1952).

Discussion

Some discrepancies exist in the description of specimens of *Pleurobranchaea* from New Zealand. For instance, in the diagnosis of *P. novaezealandiae*, Cheeseman (1878) stated: "branchial plume often over an inch in length, and free for half that distance; pectinations about 17, finely ciliated." This number of pinnae is well below the average (23) for the species based on material I have examined, but the distal pinnae are so small Cheeseman probably missed them in his count.

Quoy & Gaimard's (1832) original figure of *Pleurobranchaea maculata,* later reproduced by Pilsbry (1896), Vayssière (1901) and Suter (1915), was inexact. It was drawn from a moribund, or dead, specimen as evidenced by the everted penis. Vayssière (1901) gave a detailed account of the reproductive system, jaws, and radula of the type material, all of which correspond well with the same organs for New Zealand specimens. Cheeseman's (1878, 1879) original illustration of *P. novaezealandiae,* reproduced subsequently by Pilsbry (1896), Vayssière (1898) and Powell (1979), is slightly inaccurate too; the mantle appears not to be confluent with the oral veil, but this is merely due to the angle from which the animal has been drawn.

Bergh (1900) originally differentiated *Pleurobranchaea novaezelandiae* var. *granulosa* on the basis that the back and tail were covered with small, round and oval granulations (0.5–1.0 mm diameter). This difference in surface texture only reflects the degree of variation of this character in *P. maculata* and it is accentuated by the fixation procedure adopted. Baba (1937) realized this and included *P. novaezelandiae* var. *granulosa* in *P. novaezealandiae*. Other differences do exist between var. *granulosa* and *novaezealandiae* according to Bergh (1900) in the shape of the jaws and ampullae of the salivary glands; but these differences do not merit taxonomic separation. They can be explained by intraspecific variation and by fixation techniques respectively. Bergh gave no illustration for his single specimen from French Pass. I have examined specimens in the Suter Collection (National Museum of New Zealand) from Te Onepoto, labelled as *P. novaezealandiae granulosa,* and can find no consistent differences from typical *P. maculata.*

Pleurobranchaea maculata is similar to the Mediterranean species *P. meckelii*, but there are several points of difference: sexually mature *P. meckelii* has a caudal spur, there is none in *P. maculata*; in *P. maculata* the retractor muscle is attached posteriorly to the floor of the body cavity whereas in *P. meckelii* it is attached to the body wall dorso-laterally; there is a significantly greater number of denticles (11–15) along the anterior edge of the mandibular elements in *P. meckelii*; the shape of the rachidian tooth is also different in the two species. *Pleurobranchaea maculata* differs from *P. californica* in details of the radula and reproductive system.

An Ectoparasitic Nematode from *Pleurobranchaea maculata*

Whilst examining the external features of specimens of *Pleurobranchaea maculata* collected from beneath subtidal stones in Leigh Harbour (23 Nov. 1973), I discovered that the slugs each carried several ectoparasitic nematodes. One had 18 nematodes, most were on the undersurface of the foot with a few on the mantle, none was on the rhinophores, oral veil or gill. Later I found more than 30 embedded in the foot sole of a *P. maculata* from Goat Island Bay.

The nematode has a long and relatively broad body which is bent to form a loop. There are pronounced adhesive organs on the tail. Specimens had their tails buried a few millimeters in the *P. maculata* tissue, and when removed most carried away some mollusc flesh.

Dr. W. C. Clark examined the nematodes and kindly informed me they probably belonged to the order Monhysterida but this could not be confirmed because all were immature. The presence of these nematodes on *Pleurobranchaea maculata* raises questions regarding their life history patterns and possible specificity.

KEY TO NEW ZEALAND NOTASPIDEA

1. Shell external, circular and flattened, limpet-like; body large and warty .... *Umbraculum sinicum* (Gmelin, 1791)

   Shell internal or absent; body elongate, slug-like 2

2. Shell present beneath mantle; rhinophores arise together; mantle large, smooth; simple border to oral veil 3

   Shell absent; rhinophores widely separated, at sides of head; mantle small, greyish, its surface puckered and wrinkled; anterior border of oral veil with numerous branched papillae .... *Pleurobranchaea maculata* (Quoy & Gaimard, 1832) Fig. 57

3. Shell relatively large (up to ½ body length), auriculate; radular teeth simple, without denticulations 4

   Shell relatively small (1/5 to 1/4 body length), triangular; radular teeth with a series of denticulations on posterior margin; mandibular elements (generally) smooth; prostate gland present; mantle lemon-yellow to apricot with scattered white specks; no pedal gland on sole of foot .... *Berthellina citrina* (Rüppell & Leuckart, 1828) Figs. 1, 5

4. Mantle uniform in colour, dull orange or creamish-yellow with a few white specks; mandibular elements denticulate 5

   Mantle spotted with large, chocolate-brown blotches; anus at rear of gill membrane; mandibular elements smooth .... *Berthella ornata* (Cheeseman, 1878) Figs. 20–22

5. Mantle with numerous, large pores; shell calcareous; anus near front end of gill membrane; mandibular elements cruciform with denticulate blades; prostate gland absent, found intertidally and shallowly subtidally (to ca. 20 m) .. *Berthella mediatas* (Burn, 1962)

   Mantle smooth, not conspicuously porous; shell very large, cuticular and without calcification; anus at rear of gill membrane; mandibular elements oval with denticles on anterior border; prostate gland present; occurs only in very deep water (>1000 m) .... *Bathyberthella zelandiae* Willan, gen. et sp. nov.

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APPENDIX

This Appendix lists the New Zealand pleurobranch material that I have examined during this study. Habitat data are included where possible. Molluscan collections housed in the National Museum of New Zealand, Wellington (NM), New Zealand Oceanographic Institute, Wellington (NZOI), Auckland Institute and Museum (AIM), and Geology Department, University of Auckland (AUG), have been inspected. Dr. M. C. Miller of the Zoology Department, University of Auckland, has generously given me access to his opisthobranch collections. Comparative Australian material was kindly provided by Mr. R. Burn of Victoria. I collected most of the live specimens on which the morphological descriptions here are based, both intertidally, and subtidally by scuba diving, and these are signified by the letters "R.C.W." in this Appendix.

Berthellina citrina

NORTH ISLAND: Spirits Bay, Northland—1 washed live on to beach near Pananehe Island, R.C.W., 14 Jan. 1972; 18 m, Black Point, N.E. side of Karikari Pen.—2 copulating, and a freshly-laid egg coil, R.C.W., 11 Feb. 1978; 10 m, off N. side of Jolliffe Point, Matai Bay, N. end of Doubtless Bay—1 beneath a stone, sand substrate, R.C.W., 30 March 1978; 11 m, off S.W. side of Motutapere Is., Cavalli Is.—1 beneath a stone, R.C.W., 29 Dec. 1978; 8.5 m, large bay at N. side of Hamaruru Is., Cavalli Is.—1 beneath a stone, R.C.W., 31 Dec. 1978; 15 m, Nursery Cove, Aorangi Is., Poor Knights Is.,—abundant on undersides of stones and also several copulating pairs, beneath kelp forest; 20 m, entrance to Riko Riko Cave, Aorangi Is., Poor Knights Is.—4 on undersides of stones, fine bryozoan substrate, R.C.W., 10 Dec. 1973; 15 m rock slope to left of Riko Riko Cave, Aorangi Is., Poor Knights Is.—abundant on undersides of stones, R.C.W., 31 Dec. 1978; 60 m, off Deep Water Cove, Bay of Islands—1 shell, dredged in grey, muddy ooze, R.C.W., 7 April 1973; 6–8 m, off Castle Rock, Taurikura, Whangarei Hbr.—1 dredged amongst deposit of *Glycymeris, Pecten, Oxyperas, Tawera,* some fine broken shell and small stones, also ascidians, bryozoans and hydroids, M. C. Miller, 18 May 1961; McGregor's Bay, Whangarei Heads—2 on 14 May 1961 and 3 on 5 May 1961, both M. C. Miller; High Is., Whangarei Hbr.—on undersides of rocks at low water level, 2 on 14 Jan. 1959, 3 on 15 May 1961 and 3 on 15 Dec. 1961; Ocean Beach, Whangarei Heads—4 (including one copulating pair), beneath intertidal stones, M. C. Miller, 14 Dec. 1961; 15–16 m, Northern Bay, Little Barrier Is.—2 on undersides of stones, R.C.W., 25 Jan. 1977; 15–18 m

"Sponge Garden" and "North Reef," off N.W. tip of Goat Is., Leigh—2 on 7 Aug. 1973, 22 on 11 May 1974, 5 on 14 May 1974, 6 on 21 Sept. 1975, 1 on 27 May 1976, several on 28 Sept. 1976 and several on 29 Sept. 1976, all R.C.W., 20 m, "The Canyon," at S.E. corner of Goat Is., Leigh—2 and several spawn coils, R.C.W., 24 Dec. 1975; "Echinoderm Reef Flat," Goat Island Bay, Leigh—5 on 19 Dec. 1960, 3 on 28 Aug. 1961, 2 on 26 Oct. 1961, and several on 21 May 1967, M.C. Miller; "Echinoderm Reef Flat," Goat Island Bay, Leigh—1 on 14 May 1974, 9 on 24 May 1974, all R.C.W., all specimens found on undersides of stones and rocks in shallow pools and channels near low water mark; 12–15 m, near "Knot Rock," c. 100 m offshore from W. end of Goat Island Bay, Leigh—2 on 25 June 1977, 1 on 5 July 1977, 3 on 29 Aug. 1977, and 1 on 20 Sept. 1977, all R.C.W.; 3–4 m, Leigh Hbr.—9 on 22 Nov. 1973 and 4 on 14 March 1974, all found on the underfaces of stones on substrate of gravel and coarse sand, R.C.W.; 4.5 m, Matheson Bay, Leigh—1 and spawn coil, R.C.W., 19 Jan. 1976; Ti Point Channel, Leigh—4 on undersides of stones, on coarse sand-gravel substrate, R.C.W., 16 May 1974; 43 m, Aldermen Is.—1, 21 Nov. 1971 (NM); 59–74 m, off E. side of Mayor Is.—1 shell, amongst pebbles, shell grit and algae, 22 Jan. 1979 (NM); Omaio Bay, E. Bay of Plenty—1, R. K. Dell, 12 March 1962 (NM); little bay before Cape Runaway, East Cape—1, on underside of an intertidal stone, K. R. Grange, 29 March 1975.

Berthella ornata

NORTH ISLAND: Henderson Pt., S. end of Rarawa Beach, Northland—1 on underside of a low-tidal, weed-covered rock, R.C.W., 18 Jan. 1970; Mahinepua Peninsula, near Whangaroa—1, R.C.W., 7 Jan. 1966; "The Gap," Mahinepua Peninsula, near Whangaroa—2 on undersides of stones in the sublittoral fringe, R.C.W., 7 Jan. 1970; Church Bay, Tutukaka—4 on undersides of low-tidal stones, J. D. Willan, 17 Oct. 1970; Pacific Bay, Tutukaka—1 on underside of a stone, E.L.W.S. level, C. Grange, 8 March 1974; High Is., Taurikura, Whangarei Hbr.—3 on undersurfaces of rocks at low-water mark, 7 Jan. 1958, 1 on 14 Jan. 1959, 2 on 16 Jan. 1959, several pairs copulating on 13 Dec. 1961 and 2 on 15 May 1961, all M. C. Miller; 6 m, E. side of High Is., Taurikura, Whangarei Hbr.—1 on undersurface of a stone, R.C.W., 21 June 1975; McGregor's Bay, Whangarei Heads—1 beneath an intertidal stone, M. C. Miller, 14 May 1961; "Echinoderm Reef Flat" Goat Island Bay, Leigh—3 on 28 Aug. 1961 and 1 on 26 Oct. 1961, both M. C. Miller, and 1 on underside of a stone on substrate of clean, coarse sand, middle of low-tidal platform in a rock pool, 22 May 1974 and 9 on 24 May 1974, both R.C.W.; 6 m off Goat Is., Leigh—1 on underside of a stone on substrate of coarse gravel and sand, D. Rowe, 30 June 1974; 12–15 m near "Knot Rock," c. 100 m offshore from W. end of Goat Island Bay, Leigh—1 on underside of a stone, R.C.W., 29 Aug. 1977; Omaha, Leigh—1 on underside of a low-tidal stone, E. N. Gardner, 16 Sept. 1974; Kawau Is., Hauraki Gulf—1, C. Wormald, 13 Aug. 1967; Beehive Is., off Kawau Is., Hauraki Gulf—1, R.C.W., 26 Sept. 1965; Mahurangi Is., off Waiwera Beach—1 on 30 Aug. 1969, 8 on 12 Jan. 1974, 1 on 22 July 1974 and 1 on 15 Sept. 1974, all on undersides of stones in pools, at low-water level, R.C.W.; 11 m, eastern side of Tiritiri Matangi Is., Hauraki Gulf, 1 on underside of a stone, R.C.W., 29 Feb. 1976; Army Bay, Whangaparoa Pen.—2 under a rock ledge. E.L.W.S. level, in a rock pool, under *Cystophora retroflexa*, R.C.W., 10 Jan. 1974; Takapuna, Auckland—1, H. Suter (Suter Colln., NM M17843); Beacon Rocks, Mount Maunganui, Bay of Plenty—2 shells, E. N. Milligan (AGU): Breaker Bay, Wellington—1 under a stone in brown algal association, W. R. B. Oliver, 15 Sept. 1923 (W. R. B. Oliver Colln., NM).

SOUTH ISLAND: Headland Pt. Portobello Pen.—1 on 21 Aug. 1962, crawling across muddy floor of a cave, 0.3–0.5 m below low-water level, and 1 on 22 Aug. 1962, on undersurface of a rock at low-water level, both M. C. Miller.

Berthella mediatas

NORTH ISLAND: Ocean Beach, Whangarei Heads—1, M. C. Miller, 14 Dec. 1961; High Is., Taurikura, Whangarei Hbr.—2 seen but only 1 collected, on undersurface of a rock, low tide level, M. C. Miller, 16 Jan. 1969; "Echinoderm Reef Flat," Goat Island Bay, Leigh—1 on the underside of a stone, E.L.W.S. level, R.C.W., 1 June 1977, and 1 in holdfast of *Laurencia* sp. in a rock pool on inner part of reef, R.C.W., 23 June 1979; Army Bay, N. side of Whangaparoa Pen.—4 on undersides of low tidal stones in rock pools, R.C.W. and J. D. Willan, 10 Jan. 1974; Takapuna, Auckland—1, H. Suter (Suter Colln., NM M17843; specimen in lot with 2 *Berthella ornata*); Narrow Neck Reef, Auckland—1 spawning, H. Suter, 24 July 1906 (NM); Cape Egmont, Taranaki—1 on underside of low-tidal stone, K. R. Grange, 16 July 1974; Pencarrow Head, Wellington—2, W. F. Ponder, 20 Oct. 1956 (NM); Point Howard, Wellington—1, W. F. Ponder, 11 Nov. 1958 (NM); Lyall Bay, Wellington—4, R. K. Dell, 8 Jan. 1950 (NM).

SOUTH ISLAND: Cape Three Points, Akaroa—4 on 17 May 1962, 1 on 18 May 1962 and 1 on 22 May 1962, all on undersurfaces of rocks at low tide level, M. C. Miller; Aquarium Pt., Portobello, Otago Hrb.—4 on 17 Jan. 1961, 1 on 18 Jan. 1961 and 1 on 17 Aug. 1962, all on undersurfaces of rock at low water level, M. C. Miller; Quarantine Is., Portobello, Otago Hbr.—2 amongst moveable stones in a sheltered inlet, M. C. Miller, 20 Aug. 1962.

CHATHAM IS: East Bay, South East (Rangatira) Is.—1 under a stone, in low tidal rock pool, E. C. Young, 2 Jan. 1975.

Pleurobranchaea maculata

NORTH ISLAND: Russell, Bay of Islands—1, L. J. Mather, May 1965 (NM); 6–8 m, S. of Castle Rock, Tutukaka—1 on substratum of coarse broken shell and sand, M. C. Miller,19 Jan. 1959; N. end of Oakura Beach—1 on underside of a stone at low tide, M. C. Miller, 17 Jan. 1960; beach at end of reclamation, near channel, N. side of Tutukaka Hbr.—1 crawling on mud amongst rocks; low water level, K. R. Grange, 14 May 1972; 8–10 m, "Waterfall Reef," coast near Goat Is., Leigh—several small juveniles on undersides of stones on 26 March 1977 and many on 22 Dec. 1978, both R.C.W.; 18–20 m, "Deep Point" and "The Canyon" at southeastern tip of Goat Is., Leigh—2 and several egg masses on 21 Sept. 1975, 1 juv. on 24 Dec. 1975, many and fresh spawn on 4 June 1976 and many on 12 Dec. 1978, all R.C.W.; 9–17 m, "North Reef," off N.W. tip of Goat Is., Leigh—1 on underside of a stone on 11 May 1974 and 1 juv. on underside of a stone on 7 May 1977, both R.C.W.; 18 m, "Sponge Garden," off N.W. tip of Goat Is., Leigh—2, R.C.W., 28 Sept. 1976; 6–7 m, off S.W. tip of Goat Is., Leigh—1, D. K. Rowe, 30 June 1974; "Echinoderm Reef Flat," Goat Island Bay, Leigh—2 on undersurfaces of stones at low-tide level, 28 Aug. 1961 and several seen on undersurfaces of rocks, in pools just above low-tide level, 26 Oct. 1961, both M. C. Miller; 3 m, Leigh Hbr.—5, R.C.W., 22 Nov. 1973; 9 m, Matheson Bay, Leigh—many, R.C.W. and M.S. Leighton, 21 Dec. 1978; 2–3 m, Ti Point Channel, entrance to Whangateau Hbr., Leigh—1 on 14 May 1974 and 1 on 22 May 1978, both R.C.W.; Mahurangi Is., Waiwera—many on undersurfaces of low-tidal stones in pools, 30 Nov. 1973 and many in similar habitats on 12 Jan. 1974, both R.C.W.; Army Bay, N. side of Whangaparoa Pen.—2 on undersurfaces of stones in low-tidal pools on 27 Dec. 1973 and many in similar habitats on 10 Jan. 1974, both R.C.W.; Matakatia Bay, S. side of Whangaparoa Pen.—1 on undersurface of a stone in a low-tidal pool, R.C.W., 30 Nov. 1973; Surfdale, Waiheke Is.—8, R.C.W., 25 Nov. 1973; 5–6 m, between Waiheke Is. and Pakatoa Is.—1, P. R. Bergquist, 14 March 1974; 8–9 m, Rakino Channel—1 on substratum of mixed shell and sand, M. C. Miller, 16 Nov. 1960; Rangitoto Channel, off North Head—1 and several spawn masses, M. C. Miller, 16 Sept. 1967; Takapuna Beach—1, H. Suter (Suter Colln., NM); West Tamaki Reef, Waitemata Hbr.—1 on underside of a stone at low-tide level, M. C. Miller, 8 Dec. 1962; Tamaki Str.—1 in bottom fish trawl, W. Tong, Sept. 1974; bay E. of Little Blowhole, South Head, Manukau Hbr.—1 found at E.L.W.S. level, D. Brambley, 2 Sept. 1966; 4.5 m, Bowentown entrance, Waihi—W. Salmons, Oct. 1977; 14 m, approx. 1.2 km offshore from Tataraimaka Historic Site Headland, S. of New Plymouth, Taranaki—1 juv. on undersurface of a stone, J. Nicholson, 15 Feb. 1978 and 1 juv., amongst fouling hydroids and algae on buoy rope, close to surface, R.C.W., 5 May 1978 and 6 juvs., 10.5–12 m on undersurfaces of stones, R.C.W., 4 July 1979; Island Bay, Wellington—1, N. M. Adams, 5 Oct. 1970 (NM); Lyall Bay, Wellington—1, C. Hale, Nov. 1952 (NM); 120 m, Cook Str. trawling grounds, 1 taken by M. V. "Thomas Currell," 27 Feb. 1964 (NM).

SOUTH ISLAND: Tasman Bay, Nelson—1, M. Young, Nov. 1934 (NM); 12 m, Golden Bay, Nelson, N. Z. Marine Dept. (NM); Port Underwood, Marlborough Sounds—3, R. Ponder, May 1962 (NM); Port Levy, Banks Pen.—1, W. R. B. Oliver, 1 April 1907 (Oliver Colln., NM); Te Onepoto, Lyttelton—1 (Suter Colln., NM); 8–12 m, off Middle Headland of German Bay Hill, Akaroa Hbr.—2 on substratum of mud and coarse, broken shell, M. C. Miller, 11 May 1962; Cape Three Points, Akaroa Hbr.—several under stones at low water, and crawling amongst algae below low water, M. C. Miller, 22 May 1962; Oputereinga Pt., Akaroa Hbr.—1 in a large pool amongst mussels, M. C. Miller, 20 May 1962; Yacht Club shore, Akaroa Hbr.—several on undersides of stones, M. C. Miller, 21 May 1962; 280 m off Cape Campbell—1, F. Abernethy, 14 Nov. 1962 (NM).

STEWART ISLAND: Golden Bay, Paterson Inlet—1, R. K. Dell, 29 Oct. 1948 (NM); 7 m, Big Glory Cove, Paterson Inlet, M. V. "Munida" Stn. 67–37. E. J. Batham, 15 Feb. 1967 (NM); 20 m off southern corner of Native Is., Paterson Inlet—1 and several spawn masses, R.C.W., 8 Feb. 1977.